Functions of calls in a tropical duetting bird species, the Yellow-breasted boubou (*Laniarius atroflavus*)

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PhD Thesis

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Contents

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Abstract

The highly developed acoustic communication systems of birds have become popular within the field of bioacoustics research. Due to a bias in research efforts the temperate zone has been the focus of most research into bird song where, typically, the males sing in order to defend a territory or attract females. However, this temperate zone bias is not representative of many tropical living bird species, with over 360 bird species, most of which living in tropical regions, performing duets whereby the males and females sing together in a coordinated manner, serving multiple functions in either a cooperative or conflicting situation. The diversity of acoustic communication is enhanced by both species specific repertoires as well as sex specific vocalisation types. Different song types can be used for specific functions, such as aggressive encounters, with many having multiple functions. When used for aggressive purposes, signal meaning can be enhanced through the use of matching behaviours, a sophisticated use of a vocal repertoire. In addition to the array of vocalisation types used, propagation properties of these are also important in regards to the intended receiver of a signal and how this is carried through the environment. Climate change as well as human induced changes to a habitat can have drastic effects on the overall transmission of a signal and could potentially change the way in which a species communication network works.

In this dissertation thesis I have examined various aspects of the sex specific acoustic repertoire of the duetting Yellow-breasted boubou, an endemic species of the Afro-montane region of Western Cameroon and Eastern Nigeria. The first area of examination was the natural vocalisation activity of the study species which highlighted the male dominant vocal behaviour and the use of sex specific repertoires. I then experimentally examined the intrusion into focal territories of either duets or the sex specific solo types. This suggested that female vocalisations are likely used in intra-pair communications whereas males are using vocalisations for defending a territory and their mate. A further series of experiments were used to assess the aggressive motivation of male vocalisation types. This suggested that males are able to display aggressive motivation through the use of matching behaviours as well as vocalisation type used. Finally, the propagation properties of all vocalisation types for different habitat types were examined to further assess the functions of song and call types. Male vocalisation types transmit further, adding more evidence to the intended receivers being neighbours and strangers, whereas females intended receivers are most likely their own mates. The abiotic source of noise caused by a network of streams, also has a negative effect on the propagation of signals, which is important due to the human induced habitat change occurring in this specific region.

Streszczenie

Wyrafinowane systemy komunikacji akustycznej ptaków są popularnym obiektem badań bioakustycznych. Wysiłki badaczy koncentrowały się przez długi czas na ptakach strefy klimatu umiarkowanego, gdzie zazwyczaj śpiewają samce w celu obrony terytorium i wabienia samicy. Jednak śpiew ptaków ze strefy umiarkowanej nie jest porównywalny do wokalizacji wielu gatunków tropikalnych. U ponad 360 gatunków ptaków, z których większość żyje w tropikach, stwierdzono wykonywanie duetów, w których samce i samice śpiewają razem w skoordynowany sposób. Duety takie pełnią różnorodne funkcje zarówno w kontekście współpracy jak i konfliktów. Różnorodność takiej komunikacji akustycznej jest dodatkowo wzmacniana zarówno przez repertuar specyficzny dla danego gatunku, jak i typy wokalizacji charakterystyczne dla danej płci. Różne typy śpiewu mogą być wykorzystywane do pełnienia określonych funkcji, na przykład w agresywnych interakcjach, ale wiele z nich pełni wiele funkcji. W przypadku używania śpiewu w kontekście agresywnym, znaczenie sygnału może być kodowane poprzez dopasowywanie go do sygnału rywala, co jest bardzo wyrafinowaną strategią wykorzystywania repertuaru wokalnego. Wokalizacje z różnorodnego akustycznie wachlarza sygnałów, mają też odmienne właściwości propagacyjne co ma znaczenie zarówno w kontekście wpływu środowiska na propagację jak i dla dekodowania znaczenia sygnału dla odbiorcy. Zmiany klimatyczne, jak również zmiany w siedlisku wywołane przez człowieka mogą w drastyczny sposób wpływać na transmisję sygnału i potencjalnie mogą zmienić sposób funkcjonowania sieci komunikacyjnej danego gatunku.

W niniejszej rozprawie doktorskiej badałam różne aspekty specyficznego dla płci repertuaru wokalizacji duetującego dzierzyka żółtobrzuchego, endemicznego gatunku żyjącego wyłącznie górski lasach deszczowych zachodniego Kamerunu i wschodniej Nigerii. Pierwszym obszarem badań było opisanie naturalnej aktywności głosowej badanego gatunku, które wskazało na dominującą aktywność wokalną samców oraz wykorzystanie zróżnicowanego repertuaru, specyficznego dla każdej płci. Następnie przeprowadzałam eksperymentalne wtargnięcie w terytoria z wykorzystaniem playbacku duetów bądź śpiewu solo samców i samic. Wyniki pokazały, że wokalizacje samic są prawdopodobnie wykorzystywane do komunikacji wewnątrz pary, podczas gdy samce używają śpiewu do obrony terytorium i swojej partnerki. Kolejna seria eksperymentów została wykorzystana do oceny agresywnego znaczenia różnych typów wokalizacji samców. Wyniki sugerują, że samce są w stanie sygnalizować agresywną motywację zarówno poprzez dopasowywanie typów śpiewu do rywala, jak również poprzez używanie konkretnego typu typ wokalizacji. Wreszcie, zbadałam właściwości propagacyjne różnych typów wokalizacji dla odmiennych typów siedlisk, aby dokładniej ocenić funkcje śpiewu i głosów. Typy śpiewu samców przenoszą się dalej niż samic, co zwiększa prawdopodobieństwo, że ich odbiorcami są sąsiedzi i obcy, podczas gdy głównymi odbiorcami wokalizacji samic są

najprawdopodobniej ich partnerzy. Abiotyczne źródło hałasu, jakim są liczne strumienie przecinające lasy górskie, ma również negatywny wpływ na propagację sygnałów, co jest istotne ze względu na zmiany siedliskowe wywołane przez człowieka, zachodzące w tym konkretnym regionie.

INTRODUCTON

Functions of songs in birds

Signals, as used throughout the animal kingdom, are defined as something that affects the behaviour of other organisms and has evolved due to the effective outcome of the signaller as well as the effective response of the other individuals (Maynard-Smith & Harper 2004). Such signals can be tactile, chemical, electrical, acoustical, or optical (Laidre & Johnstone 2013). When a signal is received by an individual this is then identified and various types of information can be acquired, bringing about possible changes in the individuals behaviour (Seyfarth et al. 2010). Communication networks arise when signals are transmitted. A minimum of two individuals are involved, the receiver and the signaller, and this social interaction can spread to other individuals in the vicinity due to the long range transmission of certain signals and the so called "active space" in which information from a signal can be obtained (McGregor & Peake 2000).

Acoustic communication

Acoustic signals, in the form of bird song, are the main form of communication used by birds (Catchpole & Slater, 2008), with vocal signals being used for cooperation or conflict and aimed at a variety of receivers. Acoustic signals are useful forms of communication to possess as they allow for signals to travel variable distances, depending on the receiver, they can move around objects and so are not visually occluded, and they can be produced at any time of day, and so are not restricted by visibility. Birds species across the globe have evolved to produce an array of sounds which, in-turn, they are able to hear accordingly. The syrinx, which is a complex sound producing apparatus, allows birds to control volume, pitch and frequency due to the precise control of muscles (Catchpole & Slater 2008). Signals produced need to be successfully detected by the receiver, therefore selective hearing is important in these communication systems in order for individuals to acquire the correct information (Catchpole & Slater 2008). The transmission space of signals can lead to information that is acquired inadvertently through neighbours (Dall et al. 2005) with eavesdropping of information occurring. This eavesdropped information could be the quality of a potential mate or the fighting ability of a potential rival (Valone 2007). This is seen in Black-capped chickadees (*Poecile atricapillus*), where females eavesdrop competing males to assess the song quality and therefore, have a wealth of information when it comes to mate choice (Mennill et al. 2002). Neighbouring individuals of the same species can eavesdrop information, but this can extend to interspecific information transfer. Predatory species can hear

the songs of their prey species and use this to locate the target. This behaviour has been seen in Eurasian sparrowhawks (*Accipter nisus*), whereby the loud songs of prey species act as an acoustic target. However, one of the Sparrowhawks' main prey species, the Great tit (*Parus major*), has evolved to produce acoustic signals that are outside of the hearing range of their predators, therefore reducing the ability of their songs to be eavesdropped (Klump et al. 1986). Within communication systems it is important for certain signals to be more publicly available than others when utilising information transfer (Valone 2007).

When considering communication networks, the dawn chorus in birds is a major aspect, as it is the combined singing of a community of bird species (Todt & Naguib 2000). For most bird species there seems to be a peak in vocal activity at dawn (Catchpole & Slater 2008) which may reflect certain factors that are beneficial to singing at this time such as foraging and energy requirements (McNamara et al. 1987). Various factors have been attributed to why birds might have a heightened singing behaviour at this time including: climatic stability, light conditions, territoriality and female fertility (Catchpole & Slater 2008). With such high levels of group singing comes competition for acoustic space, as certain signals are masked by both inter and intra specific individuals (Belinsky et al. 2012).

It is obvious that signals have to reach the receiver effectively. Such signals have to cross a certain distance, during which time the signal is subject to degradation and attenuation (Forrest 1994). Degradation is the structural change of a signal and can occur due to physical scattering (Boncoraglio & Saino 2007) due to atmospheric turbulence which in turn affects the amplitude of the transmitting signal (Wiley & Richards 1978). Alternatively, signals can go through attenuation which is the loss of energy of a signal induced by signal absorption of the surrounding environment (Boncoraglio & Saino 2007). Degradation of a signal effects the quality of the received signal whereas attenuation effects how the signal is received (Ręk & Kwiatkowska 2016). The frequency of a song is important with regards to propagation with lower frequencies degrading less. There are certain limitations with how low the frequency of a vocalisation can be, including the hearing range of the specific species and the size of the syrinx (Boncoraglio & Saino 2007). The habitat in which birds occur can select for certain acoustic properties due to specific habitat structure and the effect this has on propagation properties (Morton 1975). This selection, known as the acoustic adaptation hypothesis, can cause differences between different species but also within species, depending on the geographic variation (Catchpole & Slater 2008). Bird species that inhabit areas of dense vegetation structure are found to utilise lower frequencies and frequency ranges to minimise the absorption and reflection of the acoustic signals via the surrounding foliage (Boncoraglio & Saino 2007). In addition to the presence of dense foliage, other abiotic factors can affect the frequencies used by certain species. Open grassland habitats with reduced vegetation are subject to wind and turbulence which also affect the propagation of

signals (Morton 1975). In addition, rain, humidity and temperature can also affect the way in which acoustic signals propagate (Sueur et al. 2019).

Difference between songs and calls

Acoustic communication in birds comes in the form of calls and songs and this difference should be highlighted here for clarification. Songs can be described as long and complex signals that are usually produced in the breeding season by males. They are typically long and spontaneous vocalisations that have specific diurnal patters (e.g. dawn chorus singing). Unlike songs, calls are short and simple vocalisations that are uttered by both sexes throughout the year. They are not produced as a spontaneous signal, but rather as a specific signal to convey a threat, flight behaviour or alarm (Catchpole & Slater 2008).

Functions of songs and calls

Bird song, especially male produced song, has two main functions: territory defence and mate attraction (Kroodsma & Byers 1991). In fact, in certain species, different songs can be produced specifically for these functions, as seen in Great reed warblers (*Acrocephalus arundinaceus*) where short songs are used for territory defence and the more elaborate song is used for mate attraction (Catchpole 1983).

Territory defence is a function of bird song that is associated with high levels of aggression, with the relative threat of another individual being assessed (Temeles 1994), otherwise referred to as the "dear enemy effect". De Kort et al. (2008) illustrate this well in their study of Banded wrens (*Thryophilus pleurostictus*), where individual males are less likely to approach high performance song behaviour due to its association with overall fitness and ability to defend a territory. A historic study on Great tits confirms this, as males with large repertoires demonstrate a "keep out" signal to rivals (Krebs et al. 1978). For discrimination between neighbours to occur, species recognition is needed so potentially aggressive interactions are directed to competitive rivals. Alder (*Empidonax alnorum*), and Willow flycatchers (*Empidonax traillii*), are species that can occupy the same habitat but have species specific songs (Prescott 1987). These two species are able to discriminate between inter and intraspecific individuals, but will act aggressively towards interspecific individuals if the certain niche is being competed for. *Streptopelia* doves are able to distinguish between different species within the genus (de Kort & ten Cate 2001). It seems as phylogenetic relatedness increases there is less response to the vocalisations by an individual. This difference has been described for ring species, where speciation has occurred due to the progressive difference of song and coincidental niche separation of species, such as the Greenish warbler (*Phylloscopus trochiloides*) (Irwin 2000).

A more specific form of recognition than that of species is that of individual recognition within a species itself. For both signaller and receiver is it important that the specific information is transferred to the correct individual. Individual recognition is when an individual is recognised and specific characteristics of the individual are associated with this signal (Tibbets & Dale 2007). Characteristics associated with an individual may be the relative threat, as costly aggressive interactions are usually towards outside stranger individuals that pose a threat to territory defence. A variety of species have been seen to show such individual recognition. Corncrakes (*Crex crex*) have been described as reacting more aggressively to stranger, rather than known-neighbour individuals (Budka & Osiejuk 2013). Similarly, both Chiffchaffs (*Fringilla coelebs*) and Willow warblers (*Phylloscopus trochilus*) are able to discriminate individual males and it seems repertoire size does not affect the ability for a species to make this judgement (Jaška et al. 2015).

In addition to recognition of a species or rival individual, the way in which a repertoire is used is important in signalling aggressive intension. One of the important aspects of song repertoire evolution are the ways in which repertoire units are used during interactions with other individuals (Beecher et al. 2000). One of the most interesting phenomena in this context is the sharing of repertoires between individuals within a population and song matching. Song matching is a form of vocal matching which can be defined as an interactive process in which an individual intentionally produces an identical (or very similar) signal as any other individual to whom the signal is addressed (King & McGregor 2016). Such a system enables the transmission of the signal towards a particular receiver as well as providing information about the motivation of the signaller (Searcy & Beecher 2009). This type of behaviour occurs in many different animal groups, including cetaceans (King et al. 2013). The assumption of the song matching system is a conventional character of such communication (Vehrencamp 2001; Akçay et al. 2013). It means that producing a particular type of signal does not involve any particular cost in comparison to the other, which would result, for example, from the fact that it is more energetically costly to produce. The evolutionary stability of such a communication strategy is due to the costs associated with the sender's response. For example, if matching the song type of an intruder (Akçay et al. 2013) or any other conventionally relevant acoustic signal (e.g. Ręk & Osiejuk 2010) informs about higher aggression, the potential cost for the sender is getting involved in a physical fight. Hence, signalling readiness to fight is only worthwhile if the sender honestly signals its physical strength or motivation to defend resources (Guilford & Dawkins 1995). Such systems have indeed been shown experimentally, but we still do not know how widespread they are and what factors promote their evolution. One of the reasons for this is the scarcity of research

conducted on different model species, as the sharing and matching of repertoires can be substantially different between species and even between different populations of the same species. Even in the best studied model, the Song sparrow (*Melospiza melodia)*, different research presents dissimilar results, most likely because populations with a different ecology differ in the way they communicate (compare Akçay et al. 2013 with Searcy et al. 2013). Moreover, song sharing and matching may also be a result of different processes. For example, different song units may have different functions resulting from its structure (Byers 2017) or they may be stochastic results of learning and dispersal processes without any obvious effect on male-male interactions (Podos & Warren 2007).

In addition to territory defence, mate attraction is a function of bird song that highlights its use in intersexual selection. Females of various species have been shown to use bird song as a way of choosing a male mate, this has been seen in Pied flycatchers (*Ficedula hypoleuca*) where singing males are preferentially chosen over non-singing males (Eriksson & Wallin 1986). Females select males on their songs based on geography and dialect, repertoire and syllable usage as well as song length (Nowicki & Searcy 2005). They are able to judge the quality of a male by the use and ability of his singing performance, the production of this requires energy and therefore, other vital behaviours such as foraging are postponed, thus signalling overall fitness. Song repertoire is one way in which a female might judge a males quality. Having a repertoire means an individual's song consists of a number of acoustically different units usually referred to as syllables or song types (Snyder & Creanza 2019). In temperate birds it is mainly males that sing and - especially in species with larger repertoires – repertoire size seems to be correlated with various aspects of the sender's quality with prominent singers being preferred by females (Hasselquist et al. 1996, Reid et al. 2004, Hesler et al. 2012). On the other hand, a high proportion of bird species have a small repertoire, starting with a single song type up to a dozen or so, and individuals within such a population do not usually have a large difference in the repertoire size they possess (MacDougall-Shackleton 1997, Catchpole & Slater 2008). It seems, therefore, that not only the size of the repertoire but also its specific composition or other features may play an important role in intersexual selection (Gil & Gahr 2002). An example of this can be seen with the Savannah sparrow (*Passerculus sandwichensis*), where the use of trill syllables by males highlights their fitness and is selected for female attraction purposes (Sung & Handford 2019). Yellowhammers (*Emberiza citrinella*) not only select desirable repertoires, but it seems geographic elements affect sexual selection in this species (Baker et al. 1987). When females had the choice between male song from different populations they would choose males that had the same dialect as their fathers. However, other species do not see such selection, with White-crowned sparrow (*Zonotrichia leucophrys*) females showing not discrimination towards males from various populations (Chilton et al. 1990). The final way in which females may select a male

based upon song is the duration of the song produced. House sparrow (*Passer domesticus*) males that produce long songs are preferred by females over males producing shorter songs (Nolan & Hill 2004). This is thought to reflect the relative energy use of the different length performances, with males who produce longer vocalisations being deemed fitter by females. Similarly, Great reed warbler females are also observed as choosing males that produce longer songs, with the shorter songs being used for intrasexual competition (Bensch & Hasselquist 1992). Whether song function be due to territory defence or mate choice, various factors are changed and amplified in order for the certain signal to come across.

Tropical perspective

The majority of studies investigating bird song are conducted in the temperate zone which is a disproportionally small area in terms of total breeding birds (MacArthur 1969). The temperate zone is an area of predictable seasonal fluctuations in both temperature and resources, effecting resource defence behaviours displayed by bird species as well as the level of competition throughout the year. This is in comparison to tropical species who have no time limits due to such severe changes in surroundings (Stutchbury & Morton 2008). The tropical zone has been neglected in much research even though this is the area where highest bird biodiversity is observed (MacArthur 1969) with as many as 80% of passerine species residing in the tropics (Stutchbury & Morton 2008). This lack of geographical study has led to the formation of an incorrect definition for bird song- an elaborate vocalisation produced by males during the breeding season to attract mates and defend territories (Catchpole & Slater 2008). Odom et al. (2015) have recently described how female song is much more prevalent than previously discussed, especially in tropical regions, and that this behaviour in females is likely an ancestral trait in oscine species (Odom et al. 2014). Descriptions about ancestral breeding range movements, from the tropics to the temperate zone, have suggested that this change led to the loss of female song in certain species due to increased male competition in these regions (Price et al. 2009). It seems a large amount of bird species are now described as having female song as well as male song, with the two sexes differing in acoustic structure, rate and complexity (Garamszegi et al. 2005; Price 2015).

Duetting- What is known?

Bird species can sing together in what is known as a duet and this is described as two or more individuals who sing together with a constant time lag and specific song structure (Langmore 2002). Duetting has been described in approximately 360 species worldwide in both passerine and non-passerine families, in-fact, 40% of all bird families have been assigned at least one duetting species (Hall 2009). Certain families, such as wrens, shrikes and honeyeaters included

several duetting species however, duetting is still deemed as relatively uncommon in most family groups (Farabaugh 1982). Certain ecological and life history traits are connected with duetting species including a monogamous breeding system, tropical distribution, lack of migration, sexual monomorphism and sedentary life style (Hall 2009; Smith 1994). A recent study has explored migration and duetting and suggests that duetting evolved with the absence of migratory behaviour and the utilisation of a sedentary life-style (Logue & Hall 2014). It seems the act of migration may reduce the duration of a partnership and in-turn affect the bond and consequent duetting ability of a pair. Signals used in duets are usually precise, high amplitude, gender specific songs or calls with an aspect of temporal accuracy (Dahlin & Benedict 2013). Amplitude of the vocalisations can depend on whether the duetting behaviour is for within or between pair communication, with low amplitude songs focussing on pair commitment. Similarly, whether a duet is for conflict or cooperation behaviour will affect the temporal coordination of the duet (Hall 2009). High temporal coordination is seen as a threatening joint display displaying the level of commitment of a pair, with the level of delay in response indicating overall attentiveness and pair strength (Smith 1994). So, duetting has been described as being a signal of both cooperation and conflict and the hypotheses surrounding this behaviour acknowledge these functions accordingly (Hall 2009). Hall (2009) suggests there are 8 primary functions assigned to duetting behaviour including: (1) maintaining contact between a pair; (2) mate guarding; (3) guarding paternity; (4) ensuring reproductive synchrony; (5) preventing a partner being usurped; (6) joint territory defence; (7) signalling quality and (8) signalling commitment.

Territory defence

The majority of studies assessing the function of duetting behaviour describe the most common use as being for territory defence (Dahlin & Benedict 2014). A pair will use duets to advertise and defend their territory and in order to do this duets need to have a specific form and social structure (Hall 2004). In this occurrence duetting signals must be loud and locatable in order for neighbour and stranger pairs to receive the signal. The responsiveness of each individual within the pair should show the strength of the pair bond and therefore the likelihood of defending a territory. Pair members are often in close proximity to one another when a duet is performed for this function and they perform duets upon intrusion of conspecifics into their territory. Duets, rather than solos, performed by the rival pair will elicit a response and there should be no sex specific response to individuals, as the receiver is the pair itself.

There are many studies that represent how duets function as a form of territory defence across an array of species. The Yellow-naped amazon (*Amazona auropalliata*) responds equally to playbacks of solos and duets and there is no sex specific discrimination in terms of aggressive

behaviour (Dahlin & Wright 2012). If the duets were being utilised as a mate guarding function then there would be a heightened response to the conspecific solo vocalisations. Hall & Peters (2008) have discussed how Purple-crowned fairy wrens (*Malurus coronatus*) utilise aggressive duetting signals as a means of territory defence. Not only do pairs duet in a highly coordinated way, but they also show close physical behaviours. This physical response is also seen in the Happy wren (*Pheugopedius felix*) where mates will move closer to each other when displaying duets as a cooperative signal (Templeton et al. 2011). It seems the perceived distances of pairs plays an important role in cooperative signals. Barred ant-shrikes (*Thamnophilus doliatus*) increase their cooperative response when a dual speaker playback of a duet, rather than a single speaker playback is used. The importance of realistic experimental design is highlighted here, especially when duet function is being assessed. In certain species there may be a certain sex that leads the cooperative duet. Although there is no difference in the vocal response towards the different sexes and playback types, male Happy wrens move closer to their mate and sing more than the female, thus demonstrating the primary role of the sex (Templeton et al. 2011). Similarly, female Rufous horneros (*Furnarius rufus*) seem to be the primary cooperative duetter. Diniz et al. (2020) suggest that although there is no difference in vocal response to playback type or even the sex of the signaller, and in fact responses are quick and coordinated, females have a tendency to approach the female speaker, suggesting a female dominance in the cooperative behaviour. Territory defence duetting behaviour should occur all year round due to the year round residency of most duetting species and there should be no effect in terms of breeding status (Hall 2004). Red-backed fairy wrens (*Malurus melanocephalus*) show no such difference. They do not duet more often during the breeding stage and the males do no initiate more duets when female are fertile, again highlighting the function of territorial defence in a duetting species.

Mate guarding

Like duetting for territorial defence, if used for mate guarding, duets have a specific form and social structure. Hall (2004) provides a good overview of the type of mate guarding and descriptions of this function. Signals are loud and locatable, as the receiver is often a rival male or female, therefore the signal needs to reach beyond the focal territory. There are sex specific parts to the duets, usually with pair members reacting more to same sex rivals, in addition solo vocalisations are deemed more of a threat than a duet from a pair, so duets are performed more often towards solo vocalisations. In certain situations the response type can be related to the assessed quality of the rival individual. Mate guarding is an umbrella term for various behaviours including preventing same sex rival competition, preventing a partner being usurped and guarding paternity.

Mutual mate defence occurs when each sex responds more aggressively to same sex solos of rivals. The Subdesert mesite (*Monias benschi*) displays such behaviour with both male and female individuals producing solos and initiating duets when exposed to same sex solo playback (Seddon et al. 2002). The strength of response can differ between the sexes, and in this case, males present a much stronger response than females. This divergence in sex responses can explain the function of paternity guarding where males use duets in order to maintain their mated status (Hall 2004). Kahn et al. (2018) conducted a study where Rufous-and-white wrens (*Thryophilus rufalbus*) utilise duetting for precisely this function. Males created more duets in their partners fertile period compared to the non-fertile period and in-turn, physical guarding was also increased at this time. Paternity guarding is also seen in Red-backed fairy-wren males. Here, duetting behaviour is a signal of quality of the male and males who provide a strong and fast duet response are cuckolded less often than other males (Baldassarre et al. 2016). In fact, in this species duetting is often performed by the young, brown and therefore "unattractive males" compared to the old and brighter males. The young males use duetting as a way of achieving a mated status in the community with high extra pair copulations (Dowling & Webster 2017). As with males of a mated pair, females can also dominate the aggressive mate defence behaviour. Steere's liocichlas (*Liocichla steerii*) females use duetting as a form of mate guarding behaviour (Weng et al. 2012). They act much more aggressively towards playback vocalisations of strange females and not to males. This sex specific response is a key part of how duets function as a form of mate guarding. There seems to be a sort of scale as to how mate guarding behaviours are used. In certain species it is mutual whereas in others it is very much sex specific. Rogers et al. (2007) conducted a study where they found that females utilise aggressive duetting behaviour towards same sex rivals, however, males showed no such sex bias. It is thought that due to the female sex bias in this species, female aggression in mate defence may be due to the need for a males care for her offspring, which in this species is a limited resource. There may arise conflicting functions of duetting behaviour in different species with one sex using duets for conflict and the other for cooperation.

Other hypotheses

Duetting can be used for maintaining contact between a pair. Differences to the aforementioned functions are that signals are meant for the partner and so are often quiet but at the same time locatable and coming from a long distance. They often occur when a pair is in dense habitat and so the individuals have limited vision of their mate (Hall 2004). Logue (2007) explains how Black-bellied wrens (*Pheugopedius fasciatoventris*) utilise duetting for contact maintenance as a secondary function as paired individuals usually approach each other after duetting displays.

Another alternative hypothesis for duetting comes with reproductive synchrony in pairs. The pre-requisite for this function is that duetting behaviour occurs in the pre-nesting phase (Hall 2004). Red-shouldered blackbirds (*Agelaius assimilis*) show an increase in duetting behaviour as precisely this time, pairs are formed due to this behaviour and there are high levels of intersexual communication (Whittingham et al. 1997). It is thought this function occurs due to the lack of obvious breeding season and external cues in the tropics, where most duetting species occur. By duetting the individuals involved can show a change in hormone levels stimulating breeding behaviour (Hall 2004). A final potential function for the use of duets in birds is to signal quality of the bonded pair. The response of rival pairs related to the quality of the bonded pair and the precision of duets is important for this (Hall 2004). Hall & Magrath (2007) were able to show how Australian magpie-larks (*Grallina cyanoleuca*) duet in order to highlight the pair strength and therefore the increased threat of the pair. It seems older pairs are better coordinated than fresh pairs and are able to duet in a more precise manner, allowing for better defence of resources. Similarly, Canebrake wrens (*Cantorchilus zeldoni*) seem to have a stronger coalition with age (Rivera-Caceres et al. 2016). New pairs produce new duets using a combination of syllables in the repertoire, newer pairs have poor quality duets but the accuracy of performance improves with bond age. This precision in timing of the different duet contributions seems an important way of representing a pairs quality. Black-bellied wrens tend to duet when they are closer to each other so as to increase signal precision as there is less signal degradation between the two individuals. This signal is perceived as a strong bond by rivals and so they are less likely to try for extra-pair copulations (Logue 2007). Although these various functions are all valid, it is likely that they are not the primary function of duetting and that this behaviour did not evolve due to these functions (Hall 2004).

Multi-functional duets

Rather than deeming duetting behaviour as a signal of cooperation or conflict, research into this behaviour seems to be leading towards a multi-functional dimension (Dahlin & Benedict 2014). If duetting is for cooperation then there will be a stronger reaction to duets whereas conflict functions have a strong response to same sex vocalisations (Hall 2004). Both these functions are used by the Gray-breasted wood-wren (*Henicorhina leucophrys*) with pairs exhibiting a strong response to duets, but each sex showing heightened aggression toward same sex vocalisations (Dingle & Slabbekoorn 2018).

In addition to simple differences between cooperation and conflict in the use of duets, they can also be used for both within and between pair communication. California towhees utilise aggressive behaviours in the form of territory defence and mate guarding targeted at rival pairs and individuals, however, consequent physical movement towards the pair member suggests an

additional function for contact maintenance (Benedict 2010). Mennill (2006) suggests similar functions for Rufous-and-white wrens, who utilise territory defence and paternity guarding functions when producing duets. When in natural conditions duets are used as a contact maintenance function but in aggressive intrusions, represented by playback experiments, territorial defence and mate guarding behaviours occur (Mennill & Vehrencamp 2008).
Certain species use duetting behaviour for a wide variety of functions which can depend on the time of year in addition to other factors. The Chirruping wedgebill (*Psophodes cristatus*) sings more in the breeding season supporting the hypothesis for establishing a territory as a function of duetting behaviour. Like the aforementioned species, they too utilise duetting behaviour for mate guarding and territory defence behaviours. When reviewing the literature, it seems that the two most common functions of duetting behaviour are territory defence and mate guarding. However, secondary uses are a popular addition to this behaviour.

Bush-shrike system and introduction to study species

Bush shrikes

The malaconotidae family, made up of bush-shrikes and allies, currently has 50 described species that cover 7 different genera. Of these, the *Laniarius* genus holds the most species with 22 different ones described (Wickler et al. 2020). Boubous and Gonoleks make up the *Laniarius* genus and have African distribution. Three ecological groups have been described for this group, including forest dwellers, dense bushland and riverine dwellers as well as thorn shrub and papyrus swamp inhabitants (Harris & Franklin 2010). Certain species have limited ranges such as the Braun's bush-shrike (*Laniarius brauni*), limited to Northern Angola (Mills et al. 2011), whereas other have a large range and are found in a variety of habitats, including the Tropical boubou (*Laniarius aethiopicus* OR *major*; recently divided into two species) (Grafe et al. 2004) and Slate-coloured boubou (*Laniarius funerbis*) (Sonnenschein & Reyer 1983). Like many tropical species, bush-shrikes hold year round territories where they utilise a monogamous breeding system. The general appearance of these birds is the pale underside and darker dorsal feathers, however, certain malaconotids have bright coloured plumage. In most cases the colouration is monomorphic with little difference in size and feather colour between the two sexes. Bush-shrikes possess small repertoires that can be produced as solos or in duets. This small repertoire size is compensated for by the flexibility in duration and repetition of the vocal signals. Males usually produce tonal whistles with females producing atonal harsh notes (Harris & Franklin 2010).

Although there are many *Laniarius* species, few have been studied, especially in terms of their vocalisations and their contribution to duetting knowledge. In simple descriptions, both

the Gabela bush-shrike (*Laniarius amboimensis*) (Ryan & Cohen 2004) and Braun's bush-shrike (Mills et al. 2011) have been described as having a very simple repertoire of 4 song types that can be used in both solo bouts of for duets. There are three species that have been investigated more thoroughly in terms of vocal repertoire and duet functions. The Slate-coloured boubou have a large geographic range and are found in both forest as well as scrub habitat. They possess sex specific vocalisations with males producing four types and females just one. Vocal activity occurs throughout the day and is heard throughout the year, probably due to the year round defence of the territory (Sonnenschein & Reyer 1983). Duetting is a prominent behaviour in this species (Wickler & Seibt 1979) with three functions assigned to this behaviour. A single duet type has been attributed to breeding synchrony between a pair, two types are for territory defence and the final duet type is hypothesised as being for mate defence (Sonnenschein & Reyer 1983).

A second species, the Crimson-breasted gonolek (*Laniarius atrococcineus*), has been studied in regards to its vocal repertoire and duet functions. Like the aforementioned Slate-coloured boubou, this species has sex specific song types that are used in both a solo and duet context. Males possess 5 vocal signals with females having four, individual recognition of these signals has been suggested for this species. In addition to the sex specific songs, there are also three types that are shared between the two sexes (van den Heuvel et al. 2013). Females of this species join duets as a way of mate guarding against rival females. Males on the other hand utilise duetting for both conflict and cooperation. They mate guard, like the females, but also choose to duet for territory defence against neighbouring individuals (van den Heuvel et al. 2014a). Mate guarding behaviour demonstrated by females is sometimes a manipulation of their paired males. This species exhibits high extra pair paternity and females who have extra pair offspring have been found to form duets more often than strictly monogamous females. This behaviour is thought to manipulate their mates into a cooperative bonding behaviour (van den Heuvel et al. 2014b).

A final species well studied in terms of duetting behaviour is the Tropical boubou. This species produce solos, duet and even trios, which are produced when a juvenile bird joins a mated pair. The duetting behaviour is the most obvious vocalisation produced by this species. Vocalisations, like the other species, are sex specific and duets used the solo vocalisations. In fact, the solo signals in this species are merely unanswered duets. Male initiated duets are the most common duet type in this species even though it has a large array of 12 specific duet types (Grafe et al. 2004). There are two main functions for duetting behaviour in the tropical that include mate guarding and joint territory defence. Territory defence is demonstrated by the majority of duet types and seems the be the dominant function. A couple of duets have both

cooperative and conflicting functions and are multi-functional in use (Grafe & Bitz 2004a). A specific duet type has been studied and was found to be a specific post conflict display. This type is only produced by a winning pair and is directed to the losing conspecifics as well as eavesdropping neighbours (Grafe & Bitz 2004b). This is the first time a specific behaviour of conflict has been attributed to the use of duets in bush-shrikes. In general, bush-shrikes utilise duetting behaviour for cooperative and conflict displays and seem to have sex specific repertoires of solos in order to build such duets, regardless of distribution size or habitat type.

Fig. 1.1. An individual of the Yellow-breasted boubou (*Laniarius atroflavus*) photograph in the study area.

Yellow-breasted boubou

The Yellow-breasted boubou (*Laniarius atroflavus*) is a bush-shrike species of the Malaconotidae family (Fig. 1.1). They are found in North-west Cameroon and Southern Nigeria and are endemic to montane forests. Surveys conducted in both Mt Cameroon (Sedláček et al. 2015) and Mt Oku (Sedláček et al. 2007) (the same site as the thesis population) observed Yellow-breasted boubous at every survey point, both acoustically as well as visually, and so they have been described as common in such regions. The study site situated 5 km south-east of Big Babanki is in the Bamenda-Banso highlands (6°05′24.9″N, 10°17′41.1″E), an area described as being one of the most important bird areas in the region (Sedláček et al. 2007). The study site covered a range of 1.5km^2 of altitudes between 2050-2200m a.s.l. The main habitat in which Yellow-breasted boubous are found is montane forest dominated by *Schefflera staudtii, Carapa grandiflora* and *Ixora foliosa.* However, due to lack of protection in this part of the continent, intense logging practices have led to severe deforestation and thus, once large forest expansions are now remnant patches forming a mosaic habitat (Sedláček et al. 2007). In fact, due to such

intense deforestation practices, the Bamenda highlands are now deemed as critical in terms of the need for conservation efforts (Riegert et al. 2004). Although the study species is a montane forest endemic, and once thought to be dependent on the specific habitat, they have some habitat plasticity and are also found in disturbed forest patches, corridors and scrub land (Reif et al. 2007). Like other bush-shrike species, namely the Tropical boubou, Crimson-breasted gonolek and Slate-coloured boubou, Yellow-breasted boubous are monomorphic in size and colour. They are a medium-sized shrike with black dorsal colouration and yellow ventral colouration (Harris & Franklin 2010; Fig 1.1-1.3). Investigations into the carotenoid pigmentation of this yellow colouration has revealed that males appear to have a higher pigment concentration than females but the reflectance is not different between the two genders (Osinubi et al. 2018). At least to the human eye it appears that the two sexes have the same colouration and individuals cannot be distinguished upon their appearance. They exhibit a monogamous breeding strategy with pairs holding year round territories (Harris & Franklin 2010). The breeding season is between November and March which coincides with the dry season and has been confirmed by surveys in which eggs and nestlings were found (Sedláček et al. 2007). Brief descriptions on the vocalisations of the study species have been made. In surveys it has been observed that individuals, especially males, produced very loud songs which can be heard from great distances (Sedláček et al. 2015). In a brief description males and females were attributed to a single song type each which they use as both solos and duets, with overall duetting activity being relatively low (Riegert et al. 2004). The vocal repertoire of this species is gender specific and the males, at least in the this population, produce three song types and the females four. Further descriptions will be provided in the methods section.

Aims

The first aim of this thesis was to gain a baseline understanding of the vocalisations used by Yellow-breasted boubous of the Bamenda highlands region. This information being important for the later interpretation of experimental findings. For the natural occurring acoustic behaviours I set out to describe the various vocalisation types used by male and female Yellow-breasted boubous. In addition, I look at how these vocalisation types are used in a solo or duet context. The final aspect of baseline vocal information to assess was the potential functions of the various vocalisation types and patterns that occur.

Having gained baseline vocal information on the study species, I then aimed to experimentally test how focal males and females use the solos and duets they produce when responding to a simulated territorial intrusion, through the use of playback technique. Using both a single speaker and double speaker playback technique meant that the relative closeness of the

intruding pair, and therefore the level of threat they portrayed, could be assessed due to the level of response they gained from focal pairs. Playback of male solo, female solo and duet bouts from a double speaker playback allowed me to test whether there were any sex specific responses to intruders which would help assign functions of either joint territorial defence, or mate guarding.

After assigning basic functions regarding the use of solos and duets by Yellow-breasted boubous, I then wanted to look further into the functions of specific male vocalisation types. Male solos, male initiated duets and male led duets are the most common and loudest signals produced by the study species and so it can be assumed that these signals are directed towards neighbours and rivals that are located a further distance from the focal territory. If the different song types from the male repertoire do carry different information about the aggressive motivation of an individual, then it would be expected that a playback with a different song type should elicit a differentiated response from the territory owner. In addition, if the meaning of a song type is due to matching of signals, rather than the specific signal type used, then the strength of response to playback that matches or does not match the focal signal would suggest this.

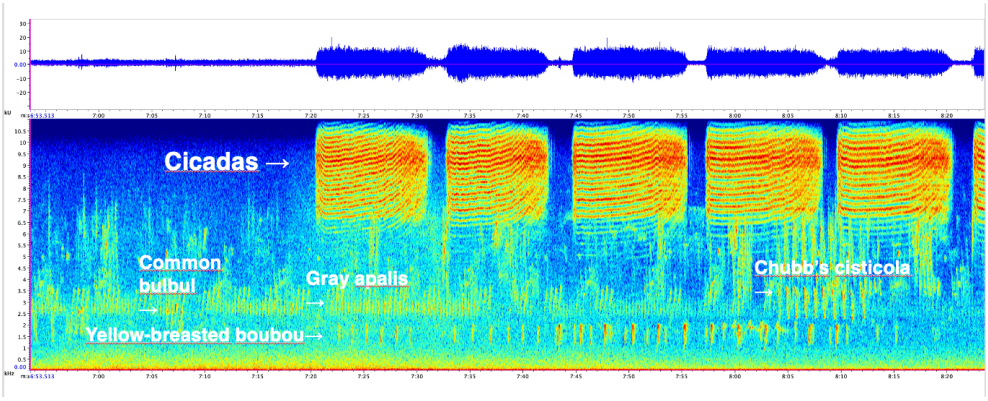

Fig 1.2. Soundscape of natural environment in the study area. Visible are both, two males of the study species as well as few other bird species and cicadas making the loudest sound but well above frequencies used by majority of birds.

The final aim of the thesis was to look at propagation properties of the various vocalisation types of the Yellow-breasted boubou and how these might relate to the functions assigned to them. The habitat of the study species is very dense meaning that often there is visual occlusion, it also has very variable environmental conditions by meaning of temperature, humidity and wind (Szymański et al. 2021). In addition, other animals in the vicinity produce loud and constant noise within the soundscape (Fig. 1.2). Due to these aspects of the habitat, it is important to look at how the different signals can propagate. In addition, the fact that the habitat is subject to much deforestation means that signals will need to adapt and evolve in order to transmit in the desired way. I aimed to assess differences in propagation between different habitat types as well as assessing the difference in transmission properties between each specific vocalisation type. An

additional propagation experiment addressed the effect of abiotic sound caused by streams within the remnant montane forest habitat and how this affects the signals transmitted and received by focal pairs.

METHODS

Study site

The West-African forests are a biodiversity hotspot due to the high concentration of endemic species found in these areas and are considered as some of the most important areas both globally and regionally in terms of biodiversity (Orme et al. 2005). In fact, the Cameroon mountains are listed as an Endemic Bird Area (EBA) for this very reason (Birdlife International 2021a), holding 28 endemic species making it one of the richest EBA's in the whole of Africa (Sedláček et al. 2007). The mountains of Cameroon are a form of archipelago (Nana et al. 2014) and are the only place in the whole of Western Africa where there is sufficient elevation and space to forge established Afromontane communities (Sedláček et al. 2007). The mountain chain is along a volcanic line found in western Cameroon (Fig. 2.1; Nana et al. 2014) and it appears that past glacial periods and the climatic stability thereafter have allowed for speciation to occur on these mountain islands, resulting in the high endemism (Reif et al. 2006).

Fig. 2.1. Map of Cameroon indicating the Mount Oku region and the mountain chain of the Bamenda highlands where the study site was located.
https://www.freeworldmaps.net/africa/cameroon/cameroon-physical-map.jpg

The study site situated 5 km south-east of Big Babanki is in the Bamenda-Banso highlands (6°05′24.9′′N, 10°17′41.1′′E), an area described as being one of the most important bird areas

in the Cameroon montane region, after Mt Cameroon and Mt Kupe (Sedláček et al. 2007). The montane region on this mountain spans between 2000 and 2950 m a.s.l. with a transition to lowlands of savannah and farmland (Birdlife international 2021a).

The specific study site covered a range of 1.5 km^2 with altitudes between 2050-2200 m a.s.l. within the montane habitat area. The habitat types that occur in the montane region include *Hyparrhenia* grasslands, pastures, forest clearings, upper montane grasslands of *Sporobolus africanus*, streams, *Gnidia glauca* woodlands, *Labiatae* and *Compositae* shrubland and montane forest habitat comprising *Schefflera staudtii, Carapa grandiflora* and *Ixora foliosa* (Fig. 2.2 - 2.5; Reif et al. 2007). The streams in this area run in a network through the study site and provide a source of abiotic noise which the Yellow-breasted boubous are exposed to. Although this montane habitat acts as an island of specific habitat requirements and niches (Nana et al. 2014) the forest has become severely fragmented. Lack of protection in this part of the continent means certain threats have prevailed in this region including: intense logging practices for fuel (Sedláček et al. 2007), forest clearance for agriculture as well as grassland grazing by sheep and goat flocks which affects the understory habitat (Fig. 2.3.; Birdlife international 2021b). Such practices have led to severe deforestation and thus, once large forest expansions are now remnant patches forming a mosaic habitat (Sedláček et al. 2007). In fact, due to such intense deforestation practices, the Bamenda highlands are now deemed as critical in terms of the need for conservation efforts (Riegert et al. 2004).

Regarding climate, West African climate is affected by two different weather fronts: the south western monsoon coming from the Atlantic; and the north easterly Harmattan wind which brings dry air from the Sahara (Jenik & Hall 1966). These two air currents ultimately cause the dry and rainy seasons in this region (Innocent et al. 2016).

Fig. 2.2. A photograph of natural rainforest habitat, the preferred habitat of the Yellow-breasted boubou.

Fig. 2.3. A photograph showing the scale of de-forestation in the Bamenda highlands. Patches occur due to human based activities of deforestation.

Fig 2.4. A photograph indicating the typical shrub habitat formed after deforestation of primary montane forest habitat.

Fig 2.5. A photograph of a typical stream location, surrounded by some of the remaining primary montane forest habitat.

In the Bamenda highlands the rainy season runs from April until October and the dry season from November until February. Although seasonality exists, these are minor in this Afromontane

region with rainfall ranging between 2400-3000 mm throughout the year, and temperature ranging between 18.7-21 °C (Innocent et al. 2016). During passive recordings using autonomous recording units (ARU), temperature (°C) and relative humidity (%) of the study site were logged through data loggers incorporated in the recording units. Data for temperature and rainfall were also collected from a local weather station, with the nearest and most precise meteorological station being located 20 km southwest of Bamenda (1250 m a.s.l.; N 5.964259, E 10.161893; see Fig. 2.6 for details). This data was collected for the exact same days as the experiments took place in order to get a proper representation of the climatic conditions (1 year between 14 December 2015 and 5 December 2016). The meteorological data that was collected during the study period corresponded well with the seasonal patterns of rainfall and temperature in the region. On average there was 2400 mm of rainfall per year and the average temperature at this time was 23 °C.

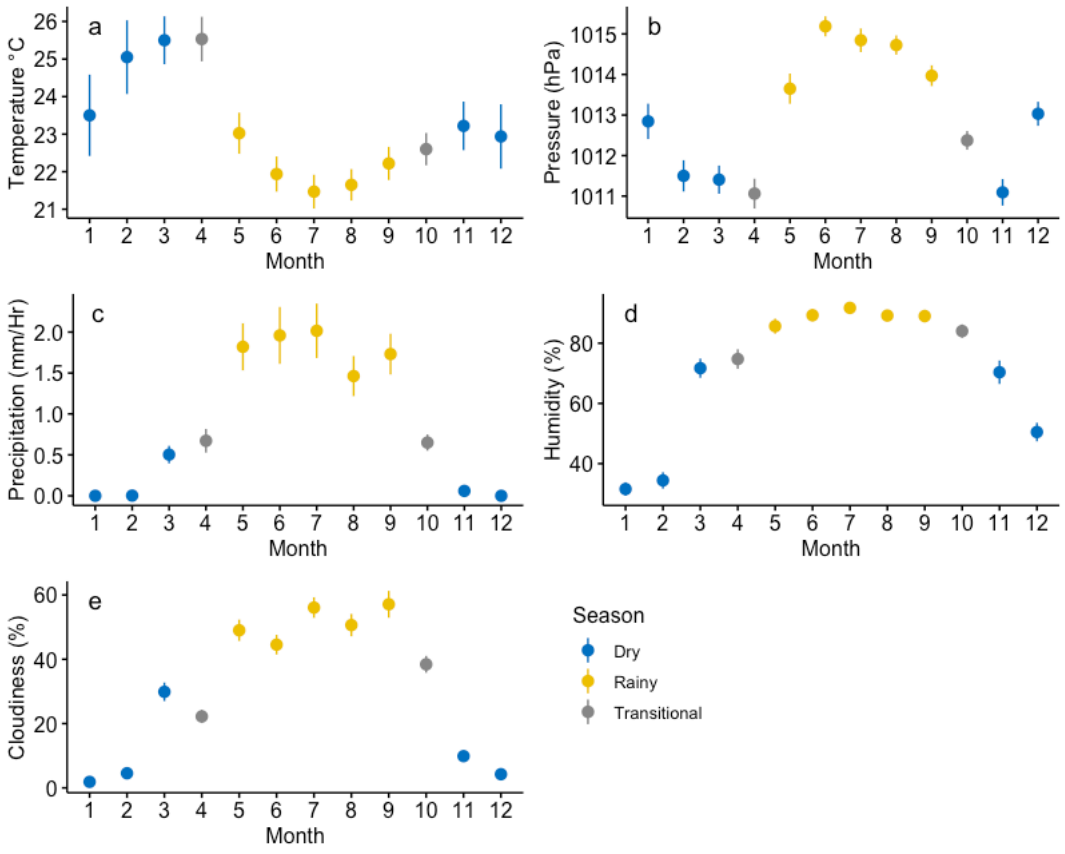

Fig. 2.6. Meteorological data characterising study area (based on the nearest station from Bamenda): (a) temperature, (b) pressure, (c) precipitation, (d) humidity and (e) cloudiness showed as daily averages with SE. Colours designate conventionally demarcated rainy and dry season with two months being transitional.

Methods of analysis of natural vocalisations

Definitions used for describing vocalisations and sound analysis

Bird vocalisations are traditionally divided into songs and calls, with songs being used for mate attraction and territory defence functions compared to a set of different but generally simpler messages encoded in calls (e.g. alarm, contact, begging etc.). In addition, songs are often longer and more elaborate vocal signals than the calls produced (Catchpole & Slater 2008). Yellow-breasted boubous produce a variety of acoustic signals that are short and relatively simple, making it difficult for classification into either a song or call category. Based on scarce literature on Yellow-breasted boubou acoustics (Riegert at al. 2004) as well as field observations and recordings, song and call terms have been established, along with the onomatopoeic naming of specific vocalisations based on their structure (Fry 2020a).

Henceforth, vocalisations and duets are described in a particular way, following suggestions presented by Hall (2009) and Logue & Krupp (2016):

– **call** – short and simple vocalisation, usually used in specific contexts such as alarm (in presence of predator), begging, etc.;

– song – vocalisations used for advertising mate or territory ownership;

– **phrase** – unit within a song, which may be an element (uninterrupted trace on sonogram) or set of elements occurring together;

– **call bout** and **song bout** – continuous call or song phrase output, where calls or phrases are separated by a silent interval (gap) lasting substantially longer than intervals between calls or phrases within the bout;

– **call type** and **phrase type** – version of call or song phrase, which could be defined on the basis of a specific (repeatable among individuals) structure;

– **duet** – coordinated singing by male and female so that their phrases alternate or overlap; in the study species duets usually consist of two or more phrases and form a duet bout, the equivalent of a 'duet train' like male-female-male-female etc. (Brown & Lemon 1979);

– **duet type** – particular combination of the phrase types used by duetting birds;

– **solo** – song bout consisting of a single or a series of phrases produced in a sequence by one individual and separated from its other vocalisations by a substantially longer time than intervals within the bout; for the study species the same phrase types were used for solos and duets and so our definition of solo is equivalent to that proposed by Logue & Krupp (2016) which is the initiation of a duet which remained without answer.

Each call and song bout can be characterised by its: duration (s), number of units (calls or phrases) produced (by a male, female or both sexes) and rate (units / min). For duetting vocalisations sex

bias can also be calculated – defined here as a ratio of female to male phrases in a single duet bout. Sex bias reflects the contribution of a particular sex to a duet train (Logue & Krupp 2016). All the mentioned above terms are illustrated on Fig. 2.7.

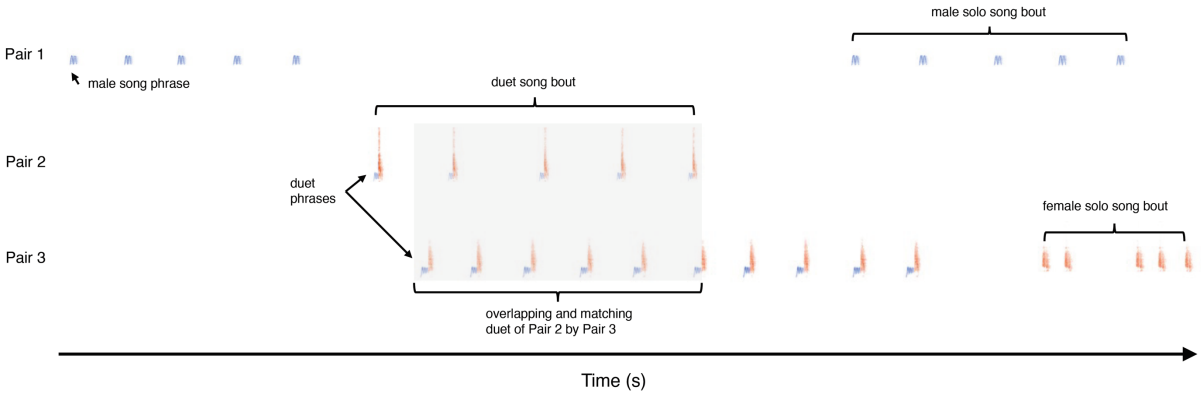

Fig. 2.7. An illustration representing a multichannel recording output from 3 separate pairs of Yellow-breasted boubous. This represents pairs producing alternating, overlapping and type matching song bouts.

Initial recordings of focal birds

In order to get an overall view of Yellow-breasted boubou acoustic behaviour, baseline recordings were collected to understand natural unprovoked vocalisation types. Spontaneously singing birds were recorded opportunistically at the beginning of the dry season (November-December) between the years 2008-17. Most of the recordings were taken in the morning (0600-1200) and evening (1600-1800) hours as these are the times accommodating the dawn and dusk chorus and combines periods of heightened activity of mountain birds . Birds were recorded with various digital recorders (Marantz PMD660, PMD661, PMD662; (Marantz, Kanagawa, Japan), and Olympus LS10, LS11 and LS12, (Olympus Imaging Corp., Tokyo, Japan)) coupled with Sennheiser ME67 shotgun microphones with a K6 powering unit and MZW67PRO windscreen (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany). Recordings were mono-linear PCM WAV files with 48 kHz sampling frequency and 16-bit resolution. After taking a recording, its time, context and geographical coordinates were noted. A few different GPS receivers (Garmin's GPSMap 76 CSx, 60 CSx and 62 Cs) were used, allowing for ± 3-6 m accuracy after averaging, depending on the current conditions (cloudiness).

The context of the specific recording provided information about the sex of the bird creating the vocalisation, the sex of the bird that started singing, and any information about what was in the background of an observation (other pair(s) or individual(s) singing or calling, and at what distance etc.).

Although Yellow-breasted boubous having a striking contrast in the yellow and black plumage, they are not easily visible in the canopy. Therefore, in the majority of situations birds

were not observed visually before recordings commenced but rather, in the first years of the study, recordings started after acoustic observation of a bird or birds that started singing or calling. The complementary context notes were useful in these situations, however, it was clear that some important information about structure and organisation of calling/ singing could be missed and so in later seasons more time was spent in particular territories, and recordings were started before the birds started to produce any vocal signals. A territory was entered and recordings were started regardless of whether a Boubou was seen or heard, even if this meant waiting for an extended period of time. This approach allowed for more adequate gathering of material and meant the full spectrum of song variety used by the birds was captured.

Microphone array recordings

In 2014 (from 12 November to 5 December) birds were recorded with eight automatic recorders (Song Meter SM3 connected with dedicated GPS receivers; Wildlife Acoustics) organised into a microphone array (Fig. 2.8). Recorders were put on trees in such a way that their microphones had active ranges covering the territories of up to three focal pairs whilst also recording their adjacent neighbours. From previous recordings that cover a 24 hour period, it is clear that this species only, incidentally, produce vocalisations at night (Budka et al. 2021; 16 points recorded continuously 48 hrs with SM1 Wildlife Acoustics song meters in 2010). Therefore, all recorders were synchronised (± 1 ms accuracy) by the GPS in such a way that they started recording at 05:00 (sunrises were between 06:06 and 06:14) and stopped recording at 19:00 (sunsets were between 17:58 and 18:01). This recording regime allowed for the recording of the entire vocal activity of the Yellow-breasted boubou pairs. SM3 units recorded a single channel soundscape with a 48 kHz frequency sampling and 16 bits quality.

Altogether array recordings were collected for 18 focal pairs, covering eight separate areas, producing a whole day activity recording using an eight-channel microphone array setup. In each of the eight areas 1-3 focal pairs were recorded with 1-2 recognised neighbouring pairs. An 8-channel microphone array was used to simultaneously record 3 pairs in 3 sessions, 2 pairs in 4 sessions and 1 focal pair in 1 session. These numbers reflected natural locations and sizes of particular territories and made it possible to place the microphones in such a way so that particular pairs could be assigned to a particular channel(s) based on the highest amplitude. If focal pairs produced vocalisations, they were always recorded on three or more channels within the microphone array.

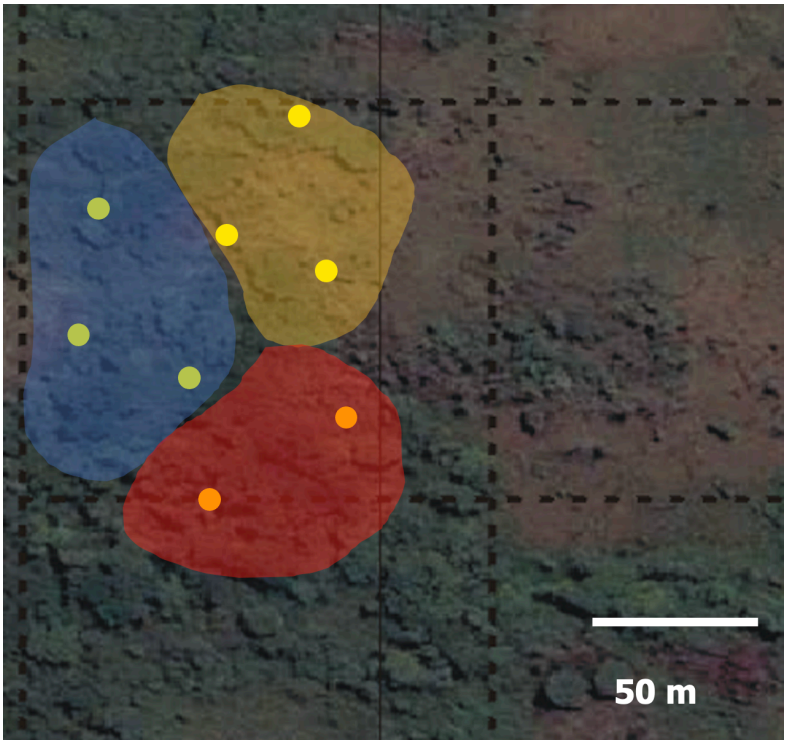

Fig 2.8. An illustration of a microphone array setup. The coloured shapes represent 3 different Yellow-breasted boubou territories. The yellow dots represent the arrangement of 8 automatic recorders. These are placed in such a way as to allow for the recording of focal territories and neighbouring territories.

Recognition of individuals

The way in which pairs were assigned to the recorded vocalisations was a multi-step process that required Raven Pro v.1.5 software (Cornell Lab of Ornithology, Ithaca, NY; http://www.birds.cornell.edu/raven) for visual investigation. The first step was to assign a vocalisation bout to a particular focal pair or to a general non-focal neighbouring pair. All recording channels from the microphone arrays were displayed together as spectrograms, and pairs were assigned based on the amplitudes of songs and calls within the channels. In short, the higher the amplitude the closer the pair are to that particular speaker, compared to other pairs, and other speakers. In order to decipher between numerous focal pairs, a simple map showing the locations of pair territories and the locations of recording devices was used as an aid. For the majority of cases there was no problem in assignment of singing pairs as birds sang from known positions within their territories, with vocalisations usually lasting for a few seconds up to several minutes (depending on the time during the day). In addition, the neighbouring pairs also responded from their own territory positions and so unique locality helps with the assignment of pair ID. In comparison to focal pairs, where vocalisations would appear on several recorded channels, birds from outside the recorded area appeared on a single (edge) channel and were easy to recognize as non-focal birds, due to the low amplitude presented on the array channels. For extra validation, a second person checked all pair assignments and if any doubt of pair ID

occurred, characteristics of a particular bout were checked. Assigning male song phrases was relatively simple as, despite possessing a shared repertoire, individual male songs have individual specificity and appear visually distinct on spectrograms. This individual characteristic of male songs was already assessed in a methodological study measuring individual identity in various species (Linhart et al. 2019). The shape of phrases was compared using the Peak Frequency Contour measurement in Raven Pro with all measurements visible on screen. If there were any doubts, measurements of frequency and time were used to separate between males. It is important to remember that for each array set up a maximum of three focal males with the addition of 1-2 neighbouring males were to be discriminated. From investigations it does not seem possible to discriminate between females based on the song characteristics and so female solo identification was solely based on location through amplitude. In such cases the preceding and followings bouts of neighbours or their own partner, make such assignments certain. Hence, the main potential error in the dataset may be a result of singing by focal females from outside of their own territories and assignment of such bouts to other pairs or non-focal birds. However, based on observations such cases are assumed to be extremely rare.

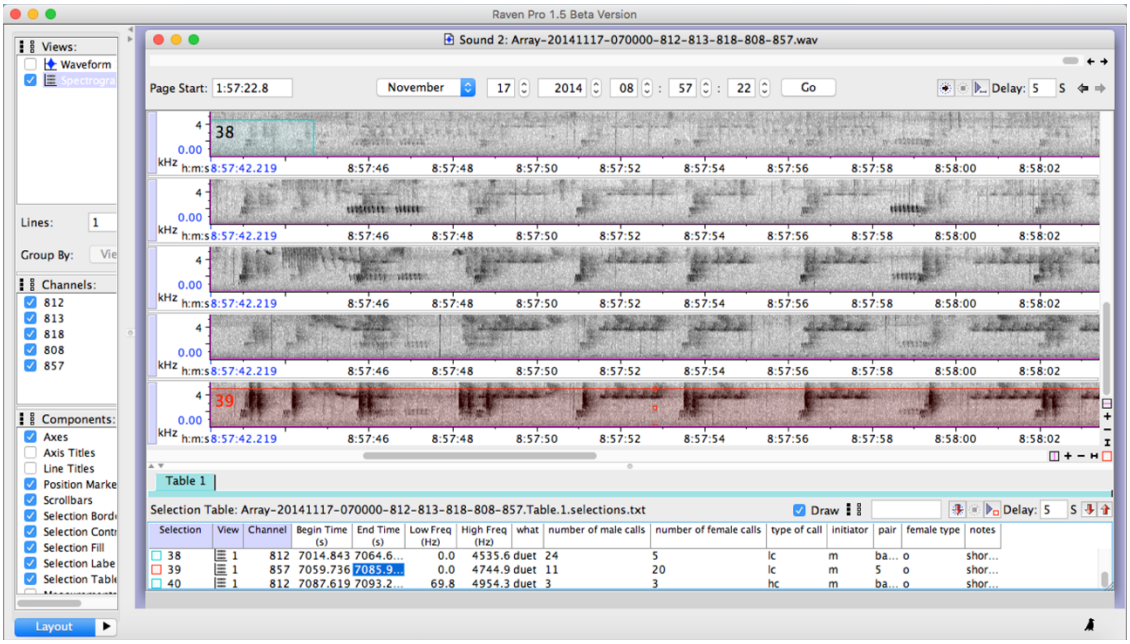

Fig 2.9. Raven Pro (Cornell Lab of Ornithology) software indicated the various microphone array channel setup. The 5 different spectrograms indicate the different microphones places around territories. The red, highlighted spectrogram is being selected as this has the highest amplitude of all recorders and indicates that, in this example, the acoustic signal is being provided by pair 5 who were utilising a duet of LC.

All call and song bouts present throughout the recordings were selected within the 8-channel setup based upon the highest signal amplitude which was from the recorder placed in the song activity centre of a particular territory. Additional annotation columns were added to each recording in a standard way and, as a consequence, each selection containing a bout included the

following information: time of the start and end (actual and in relation to sunrise and sunset time), category of bout (song or call type, solo or duet), sex of initiator, type and number of units produced by each sex, pair identity (based on location and individual song characteristics) and additional notes (Fig. 2.9). The following parameters of Raven Pro were used: Window type: Hann, 1024 samples; 3 dB Filter Bandwidth: 67.4 Hz; Time grid: overlap 50% giving Hop Size: 512 samples; Frequency Grid: DFT Size: 1024 samples giving 46.9 Hz × 10.7 ms resolution of measurements.

Analysis of recordings from microphone array setups

Variables used for describing vocalisations

Three different vocal variables were used in various models to assess the overall characteristics of the vocalisation for the Yellow-breasted boubous. The three response variables are as follows: 1) number of units in a singing bout, 2) bout duration (s), and singing rate (units/min).

Statistical analysis of natural vocalisations

To quantitatively characterise the production of male and female solos, as well as duets, basic descriptive statistics were used. I focused on the frequency of different vocalisation bouts produced by focal pairs, and quantified them by the number of phrases, duration and rate. In order to characterise the general daily pattern of vocalising I counted the number of different bout classes (e.g. call bouts, solos, duets etc.) produced by each pair during every hour of activity and with reference to the time of sunrise. In addition to descriptive statistics, I used generalized mixed models (GLMM) with a log-link function and Poisson error distribution, or identity link function and Gaussian error distribution, that included pair identity as a random factor, with time of day (hour in relation to sunrise), type of bout (solo, duet), sex (male, female) and duet initiator (male or female) as explanatory effects. All statistical analyses were performed using the program STATA/MP 16.x (StataCorp, College Station, Texas, USA). Mean $\bar{x}$ ± SE values and 95%CI are reported.

Experimental design

In order to fully investigate the functionality of Yellow-breasted boubou vocalisations, four different experiments were conducted to assess 1) the reaction towards an intrusion of a stranger (non-neighbouring) male singing a solo, female singing a solo or a duetting pair, into a focal territory (E1 and E2); 2) the reaction towards a duetting, stranger pair singing with different types

of male song in terms of contribution to the duet (E3); and 3) the propagation properties of different vocalisations used (E4). Experiments E1 and E2 were simple, noninteractive playbacks done with the use of a single speaker (E1) or two speakers (E2). The experiments in E3 were interactive with a double speaker design and improved characteristics allowing for a more naturalistic simulation of intrusion. Experiment E4 was a classic propagation experiment with a few different trials conducted in different environments.

Experiments E1 and E2: Response to duets, male solos and female solos and comparison of single vs two speaker playback design

Playback experiments were performed between the 13th November and the 5th December in 2014 (E1), and between the 18th and 27th November 2015 (E2) during the first four hours of the morning but after the dawn chorus (6:30-10:30 a.m. local time). Altogether, in each of the two experiments, 18 territorial pairs were tested three times with the playback of female solo, male solo and duets, in a fully randomized order. Different pairs were used for the experiments conducted in 2014 and 2015. The three treatments for a particular pair were done on the same day and were separated by 60-90 min.

Playback preparation for experiments E1 and E2

All songs used for playback in the experiments were recorded in November and December between 2012 and 2015 within the study area in Cameroon. Songs played to particular birds always originated from birds recorded over 500 m away from the focal pair, in order to ensure that playback stimuli were perceived as a stranger pair, female or male for each pair being tested. Individual males and females were recorded in 48-kHz sampling frequency and 16-bit resolution with a Marantz PMD670 recorder coupled with a Sennheiser ME67 shotgun microphone. Songs used were selected due to their high signal to noise ratios, classified as High whee-oo (for males) and Chock (for females). These are the vocalisations used most often by the studied species both as solos and in duets. All recorded songs were filtered (high-pass, 0.5 kHz; low-pass 16.0 kHz) before the preparation of playbacks recordings.

Each playback stimulus was created from a single male or female song (for solos) or the artificial combination of male and female songs (for duets). Each solo or duet was prepared from samples belonging to different individuals to avoid pseudo-replication and to make sure that all tested pairs were responding to unknown individuals at all times. During each treatment duets or solos were played for 2 minutes using the same, natural rate of about 1 song phrase (or duet phrase) every 2 seconds. The volume of each playback was set to 90 dB SPL at a 1 m distance from the speaker, measured with a CHY 650 digital sound level meter (CHY Firemate Co.,

Ningbo, China). Digital editing, construction and analysis of the playback files was conducted with Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, USA). Sound files were visualized with the following spectrogram parameters: window type: Hann, FFT length: 512, temporal overlap: 50%, time resolution: 5.33 ms, sampling frequency: 93.8 Hz.

Playback procedures for experiments E1 and E2

Territories were located a few days prior to when the experiments would take place and were monitored daily in order to assess whether a pair or individual birds were present. Observers simply waited for pair members to perform vocal signals. For the experimental procedure, playbacks were conducted using either a single UE Boom speaker (Logitech, Lausanne, Switzerland) placed on a branch (~2.0 m above the ground) within the focal pair territory, or two UE Boom speakers. The single speaker approach is referred to as T1 and the two speaker approach as T2. All solos in both trials were reproduced from a single channel WAV file and therefore the recording played through one of the two membranes within a speaker. The duet playback for T1 was reproduced with a male song phrase from one membrane and the female phrase from the second. By conducting the duet playback in this way, it represented a situation in which the male and female of the pair were in very close contact (ca. 15 cm), possibly perching next to each other on a branch, when singing a duet. T2 conducted duet playbacks in a different way through the use of two speakers. Each speaker would play a sex specific part of the duet, and so by separating the speakers (ca. 10 m) this provided a situation whereby the pair members were separated. Being perched together or separated within the territory are both natural situations for this species. After placing the speakers in the required locations, observers moved away from the playback arena by approximately 10-15 m. By doing this, observers were able to clearly view the playback space whilst minimising disturbance to the focal pair. In all cases, there was no approach to any speaker by the territory owner prior to the start of playback.

The experimental procedure was started if a focal pair had been observed singing prior to the setup of the experiment and on the same morning. To be sure that there was no effect of speaker presence or recording presence, the song of the European Chaffinch was broadcast as a neutral stimuli. For each of the 18 focal pairs, the experiment consisted of a 2 minute playback phase, followed by a 2 minute observation phase. One observer recorded the vocal responses of focal birds using a Marantz PMD 670 recorder coupled with a Sennheiser ME67 shotgun microphone. When dense foliage was not obstructing the view of the focal birds, a second observer would simultaneously prepare a voice commentary on each of the focal individuals behaviours. This was done on an Olympus Ls-10 recorder. The recordings of vocal behaviour were saved as PCM WAV files with a 48-kHz sampling frequency and 16 bit resolution.

Response variables used in experiments E1 and E2

I extracted eight variables measuring the behavioural response of the tested birds. For the behaviour of approaching we used three variables: (1) latency to approach the speaker (s), (2) closest distance to the speaker (m), and (3) number of flights towards or over a speaker. In the case of the double speaker playback procedure, I consider focal birds moving to either of the two speakers as approaching movements. For the vocal behaviour analysis I used: (4) latency to start vocalisation (s); (5) number of male solos; (6) number of female solos; (7) number of male initiated duets; and (8) number of female initiated duets. Duets initiated by a particular sex means that during the whole bout, phrases of a particular sex preceded phrases produced by the partner. Based on these response variables I also assigned each experiment into one of three classes concerning whether males or females responded stronger or whether there was no clear sex bias in response. In about 83% of cases there was no problem with assigning sex bias as the male or female clearly responded stronger, by producing more songs and/or coming closer to speaker(s). Alternatively, there was no bias in response. Sex bias was usually linked with solo singing by one of the birds, regardless of whether birds also sang in a duet or not. In the remaining cases we only observed duets initiated and led by males in vocal response with no clear bias in approaching. Assigning such experiments to having no sex bias or a male biased response is very arbitrary, we presented results for both approaches.

Statistical analysis of birds' responses in experiments E1 and E2

The Fisher exact test and χ^2 test with Yates' correction for continuity were used to test the effect of the experiment and treatment on evoking a response, as well as to assess any sex bias in response. The original response variables that were measured during experiments were partly correlated with each other. Therefore, to analyse the general strength of response to playback a principal component analysis (PCA) with varimax rotation and Kaiser normalisation was used. The inspection of original variables from both experiments revealed that the pattern of response variation was similar, hence a PCA was done for the combined data from E1and E2, to make later comparisons easier. The dataset was well suited for PCA (Kaiser-Meier-Olkin = 0.788, Bartlett test of sphericity = 246.452, $P < 0.001$). The first component explained 41.2% of the variance, and had heavier loadings from all variables relating to approach to speakers, duets initiated by males, and female solos (Table 2.1). This principal component is referred to as PC1 or the 'Approaching and duets' component. The second principal component explained 13.4% of the variance and had heavier loadings for the male solo response. It is referred to as PC2 or the 'Male solos' component. One of the original response variables, duets initiated by females, had low and opposite loadings on both the components axes which was probably an effect of the

rarity of this kind of response (it was only observed in 19 out of 108 trials) when spread among different experiments and treatments.

Table 2.1. Principal component loadings for pairs Yellow-breasted boubous playback responses.

Statistics and original response variables	PC1 - Approaching and duets	PC2 - Male solos
Eigenvalue	3.30	1.07
% of variance	41.21	13.41
Cumulative %	41.21	54.62
Latency to approach speaker	**0.84**	0.09
Closest approach to the speaker	**0.81**	0.15
Number of flights	**-0.74**	0.23
Latency to vocal response	**0.74**	0.11
Male solos	-0.11	**-0.93**
Female solos	**-0.56**	0.01
Duets initiated by males	**-0.64**	0.21
Duets initiated by females	-0.33	0.26

For the analysis of differences in response to the different treatments in E1 and E2 generalized estimating equations (GEE) were used. The models and parameters were selected using the quasi-likelihood under independence model criterion (for choosing the best correlation structures) and its corrected version (for choosing the best subset of predictors). Two separate analyses with PC1 and PC2 dependent variables were performed. Categorial predictor variables used were: experiment type (E1, E2) and treatment (female solo, male solo, duet), as well as the interaction between them. Pair identity was included as a random factor. All of the statistical analyses were two–tailed and were performed using IBM SPSS Statistics v. 25, SPSS, Inc. Chicago, IL). All *P* values are 2 tailed.

Experiment E3: Response to the different male-led duet types

Playback experiments were performed between the 13th of November and the 1st of December 2016. Experiments were conducted during the first 4 hours of the morning (06:30-10:30 a.m. local time). A total of 18 territorial pairs were subject to playback experiment three times, each being presented with three different duets types, in a counterbalanced random design. For each pair, the duet treatment playback was conducted on a different day, separated by 24-48 hrs. The effects of the order of duet exposure was tested. Experiments were only started when in the focal pair territory and when both the male and female of the focal pair had been present, vocally or visually, before playback. In order to avoid habituation by the focal pair, the speakers for the three different playback trials were positioned in slightly different places within the territory.

Playback preparation for Experiment E3

As described in the previous experimental procedure, this experiment used two UE Boom speakers (Logitech, Lausanne, Switzerland) to broadcast the playback recordings. The male and female phrases were played by as separate channels of WAV files using an Apple iPod Touch (model A1574, Apple Inc.). To achieve a realistic spacing between the simulated duet partners, speakers were places on branches approximately 2m above ground and separated by a distances of 9.8±0.27 m (95%CI: 9.2-10.3 m) on average. This separation of speakers allowed for the observation of sex specific responses by the focal birds and whether the behaviour was directed towards the male or female playback speaker. The volume of each playback was set to 90 dB SPL at 1 m distance from the speaker, measured with a CHY 650 digital sound level meter. Digital editing, construction and analysis of the playback files was conducted with Raven Pro 1.4.

Songs that were used as the playback duets in the experiments were from local birds to account for realistic dialect, however, they originated from pairs that were at least 1 km away from the focal bird territory to ensure that the "stranger" status was obtained. These birds were recorded at a 48-kHz sampling frequency and 16-bit resolution with a Marantz PMD670 recorder or Olympus LS-10, LS-11 or LS-12 coupled with a Sennheiser ME67 shotgun microphone. Songs with high signal to noise ratios were chosen to be used for playback. All recorded songs were filtered (high-pass, 0.5 kHz; low-pass 16.0 kHz) before the preparation of playbacks recordings. During each treatment we played duets with the same, natural rate of about 1 duet every 2 seconds. We created duets with three types of male whistle song phrases: H, L, W. The female part of duets was always built with Chock (hereafter C) song phrases which are commonly used by females both as solos and in duets. All playback of duets reflected the most common situation where a male initiates and leads a duet while a female follows the partner's phrases with a short delay and overlaps each of his phrases with a single female-phrase.

Playback procedure for Experiment E3

Based on earlier observations and preliminary experiments an interactive experimental design was utilised, reflecting natural interactions between birds and allowing for the improved measurement of responses. Birds were observed before the playback start for about 5 minutes or more (sometimes waiting for birds in a particular location for up to 60 min).

To ensure know effect of the playback noise, Common chaffinch song was played before any experimental procedure took place. When focal pairs had been observed, the playback of the 2 minute duet sequence started. This playback continued until the focal pair responded. If the focal pair started a vocal response to the duet playback then the broadcast was immediately stopped until the singing bout from the focal pair ceased. After the focal pair stopped singing the

playback resumed. This method of playback stop and start lasted as long as the 2 minute playback (~60 male and female phrases). Therefore, the playback period lasted at least 2 minutes plus any time the focal birds showed a vocal response. After the playback phase, the focal pair were observed for a further 2 minutes in the post playback phase (Fig. 2.10).

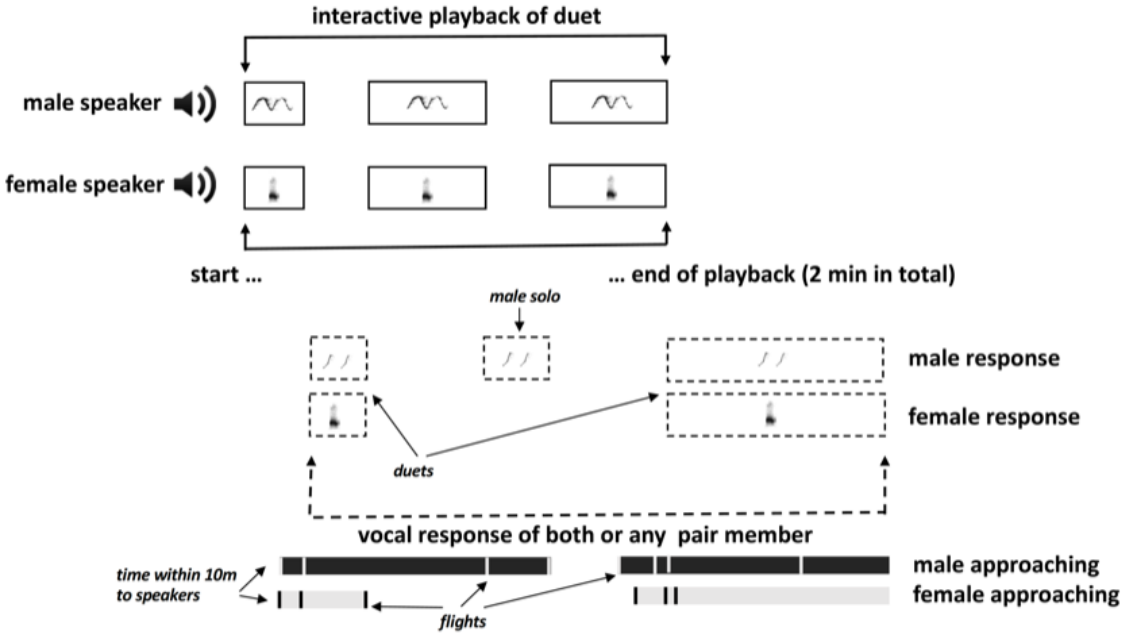

Fig 2.10. A representation of the experimental design. Duets were played back from two different speakers (one with male and one with female vocalisation type) for two minutes in total. If a focal pair member (or any pair member) started to respond vocally then the playback was paused. Playback started again once the birds had stopped responding vocally. When the playback ended, a further two minutes of recording was conducted. Simultaneously to this recording, physical responses were noted, as well as the distance to any of the playback speakers of the focal birds.

Response variables used in experiment E3

All vocal responses of the tested birds were recorded using an Olympus Ls-11 recorder coupled with a Sennheiser ME67 shotgun microphone by one of the observers positioned ca. 20 m from the speakers. A second observer was located on the other side of the speaker in a place where good observation of the playback arena was possible. This observer would dictate (using a lavaliere microphone) any focal bird response, especially any movement. This dictation was started before the start of the playback in order to assess the position of the focal birds within the territory. These dictations were later synchronised with the vocal recordings, using the beep sound at the end of the playback as a cue. Distances between speakers and the responding birds were measured with a Leica DISTO D510 laser range finder (Leica Geosystems). The closest distances to speakers, between speakers etc. were measured just after the end of experiment.

I tried to record many aspects of the focal birds' behaviour but for the aim of the analysis I limited it to those variables which I was able to collect with sufficient and repeatable certainty among all experiments. In the case of the vocal response I used number of phrases sung by males and females in duets and separately the number of phrases sung by males and females in solos. As Yellow-breasted boubous are loud there was no problem with assigning every single phrase to a particular sex and type. I also noted if responding males matched the same type of song as used for the playback. I assigned the response as matching if the male started the response with the same song type as used for the playback (in one experiment the male switched to match the playback after singing three phrases of the previously sung type). The physical behavioural responses of males and females were measured by the time spent within 10 m to speaker (s), latency to approach the speaker (s), closest approach to the speaker (m), and number of flights.

Statistical tests for Experiment E3

I present basic descriptive statistics, starting with summaries of how pairs responded to different treatments vocally and by approaching the speakers. Such binary response variables as vocal response (duet, solo), approaching or close approaching (< 10 m), as well as matching the playback type by focal male, were useful for the general description of bird responsiveness and tested with χ^2 or χ^2 with Yates' correction tests. For the quantitative analyses I analysed two vocal response measures reflecting the number of phrases sung in duets and solos, and the four aspects of approaching (latency, closest distance, time in 10 m to speakers, flights). Means are presented ± SE throughout and males and females are always treated separately. I analysed quantitative data using generalized linear mixed models (GLMM) to comply with non-normal data (Bolker et al. 2008). The response variables were log-transformed measures of vocal response (dues, solos) and approaching (latency, closest distance, time in 10 m to speakers, flights). I included the following main factors in our models: (i) playback treatment (three levels: HC, LC and WC duets); (ii) playback order (three levels: first, second or third); (iii) sex of responding bird (two levels: male or female). I used sex as a factor because duetting is not the only type of vocal activity used by the yellow-breasted boubou, and sexes may potentially respond differently to playback (Wheeldon et al. 2020, 2021). A similar approach was used in an earlier study on different duetting species (Kovach et al. 2014). I used log linear target distribution and included all first-order interaction terms, and we incorporated pair identity as a random effect. To test the effect of treatment on playback type matching, we used a GLMM with a binomial error structure and logit link function. In this analysis, only males' response variable was tested as only males might match the male-part of the playback. Post hoc pairwise comparisons were obtained through the GLMM interface with *P* values corrected for multiple comparisons using the LSD (Least Significance Difference). The models' parameter choice was based on diagnosis of response

variables distribution, inspecting the QQ plot and the lowest corrected AIC criterion, as available in GLMM panel in SPSS 26 used for these analyses.

The last aspect of bird response I focused on was song type matching. As males in the studied population share all sex-specific song types they could potentially freely decide if they respond with the same or different song type to playback. One can imagine that if males respond by choosing the song type randomly from the repertoire, the chance of matching the playback would be 33.3% (1 divided by 3 types available). However, assigning a random matching pattern to yellow-breasted boubous seems to be a very superficial reflection of natural behaviour. An earlier study showed that the song types H:L:W were not used in equal proportions (Wheeldon et al. 2020). Depending on whether I consider solos or duets, the proportions were 4:2:1 or 5:4:1, respectively. So matching song types in experiments should be compared to such frequencies.

Experiment E4: Propagation of songs and calls through the environment

Propagation experiments were conducted during the dawn hours for three consecutive days on the 29th and 30th of December and 1st of November 2017. This is considered as both the peak of breeding activity and vocal activity (Szymański et al. 2021). The first experiment assessing propagation was looking at distances of signal propagation up to 100 m. These were conducted in three different habitat types: FOREST, SHRUB and STREAM (Figs. 2.2 - 2.5). Details of the habitat types are found in Methods. The FOREST and SHRUB locations had a relatively level terrain and so the recorders and microphones were placed at the same elevation and height above ground, meaning no obstacles apart from the vegetation were blocking signal propagation. The STREAM location was in a more uneven terrain located on a hill between two streams which generated substantial noise. The places in which the recorders and playback speaker were placed were more than 10m from the streams and so were not under direct pressure from elevated noise. However, the ambient noise level for the STREAM location was higher than for the other two location types (Table 2.2). The typical terrain in the STREAM locations had ground bulges in the propagation pathway, but these reflected the most typical type of habitat in these locations, a preferred habitat type by the study species. To further this experiment, differences between the different song and call types of male and female Yellow-breasted boubous were examined using the same experimental process and same habitat locations.

A final propagation related experiment addressed how the direct stream noise affects the communication system of the study species, depending on the location of the signaller and the receiver in relation to the stream.

Table 2.2 Characteristics of propagation experiments with the Yellow-breasted boubous (*Laniarius atroflavus*).

Characteristics of propagation experiments	Names of propagation experiments used in the manuscript: FOREST	SHRUBS	STREAM	STREAM FROM	STREAM TO
Habitat	level terrain forest	level terrain shrubs, early stage of forest regeneration	hilly terrain forest located between streams	hilly terrain forest, close to stream	hilly terrain forest, close to stream
Total transect distance	100 m	100 m	100 m	25 m	25 m
Height a.s.l. (m) of propagation point ± vertical levelling of transect (m)	2141 ± 4 m	2059 ± 6 m	2026 ± 17 m	2042 ± 7 m	2035 ± 7 m
Date of experiment	29 Nov 2017	30 Nov 2017	1 Dec 2017	1 Dec 2017	1 Dec 2017
Time of experiment	6:51 - 9:25	6:50-8:47	6:53-9:21	6:53-9:21	6:53-9:21
Temperature (°C)	10.8-14.7	8.0-19.8	8.3-12.6	8.3-12.6	8.3-12.6
Humidity (%)	52-80	56-72	60-73	57-66	57-66
Ambient noise (dBA)	34-39	31-35	39-40	56-58	55-58

The noise of streams is common in the Yellow-breasted boubou study area but very patchy. The STREAM locations in the aforementioned propagation experiments were located in a forest patch with increased ambient noise duet to the presence of a nearby stream. In addition, speakers and microphones were not placed within the loudest noise areas caused by the flowing water. In this final experiment then, different "micro" locations were chosen in the STREAM location. Two situations were simulated: 1) A calling bird is located close to a stream (the source of ambient noise) with a receiver being located 25 m away and 2) a calling bird is located ~25 m perpendicular from the stream while the receiver is located directly next to the stream (Fig. 2.11). These are further referred to as STREAM FROM and STREAM TO. The first point was located (horizontally) ca. 2 m from a loud stream (58 dB) and the second point was located 25 m to it (55 dB), perpendicularly to the stream bank. Between these two points there was no terrain obstacles so only the stream noise and vegetation were the factors.

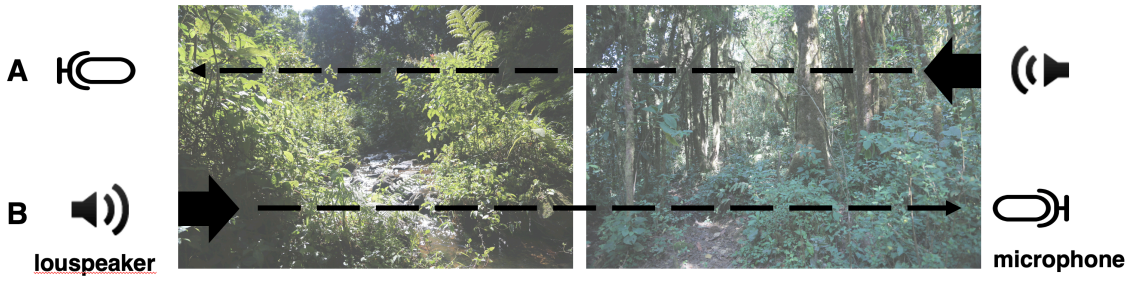

Fig 2.11: Layout of propagation experiment at stream sites. Picture A represents experiments where the signal was being produced in nearby forest and directed towards the source of abiotic noise (the stream). Picture B represents the opposite, whereby the signal was produced at the stream and directed towards the nearby forest habitat.

The point closer to the stream was in a very noisy environment and this can be compared to a bird singing while moving along a stream bank system.

Sound files for propagation playback

All vocalisations used for propagation playback were recorded between 2014-2017 using Marantz PMD660 and PMD661 portable recorders and a Sennheiser ME 67 microphone (frequency response: 40–20 000 Hz ± 2.5 dB) with windscreens. All the recordings used for the experiment were taken from 3-6m of a calling bird. Sounds were recorded as 48 kHz / 16-bit pulse code modulation (PCM) wav files.

I used 283 high quality samples of Yellow-breasted boubou vocalisations that were recorded from 24 males (4-20 per male) and 72 samples recorded from 5 females (9-20 per female). For specific male song types there were 159 H type recordings, 57 L type and 68 W type recordings. For females there were 36 C song phrases and 36 of the alarm type Keck (Q) call. The vocalisations recorded from each individual were saved and later used for playback at their natural rates. To allow for analysis of background noise there were pauses of a few seconds between consecutive male calls. The peak amplitude of each playback sample was prepared to match the natural levels of the species at 90±3 dB (A) (SPL at 1 m).

Propagation playback procedures

In order to assess how signals are modified during propagation through the habitat the songs and calls of the study species were repeatedly broadcast and re-recorded several times and from different distances. This allowed for signals to propagate between the speaker and recorder through similar but not identical vegetation.

Fig 2.12. Layout of propagation experiment at various distances. As displayed here, the signaller which in experimental terms is the loudspeaker, emits a song towards 4 recorders placed at 12.5, 25, 50 and 100m distance.

Weather conditions and ambient background noise were measured at the beginning and end of each playback session. In all three types of habitat tested, the temperature and humidity increased during the time when transmissions were done (details in Table 2.2), but these differences were not statistically significant ($P > 0.11$). The ambient noise varied between

habitats: 34-39 dB(A) in FOREST, 31-35 dB(A) in SHRUBS, 39-40 dB(A) for STREAM, and 55-58 dB(A) for STREAM-TO and STREAM-FROM.

For re-recording the transmitted signals microphones were placed at 12.5, 25, 50 and 100m from the loudspeaker (Fig. 2.12). In addition, the test sounds were also recorded in an open, quiet area at a distance of ~2m from the speaker. This was done in order to have a control to be able to compare propagated sounds with during the calculation of response measures (Details in "Sound analysis" below). The loudspeaker and the microphones were placed at 2m above ground level, reflecting the natural song post location of the study species (although variation in song post height can occur). The vocalisations detected at the various distances by the microphone are referred to as the propagated sounds.

Signals were emitted by a MacBook Air (model: MacBookAir6,2, Apple Corp.) as PCM WAV files (48 000 Hz \ 16 bits) connected to a UE Boom 2 (Ultimate Ears, Irvine, CA, USA) loudspeaker with a 9 W amplifier (frequency range 90–20 000 Hz and linear frequency response within species-specific frequency range). Recordings of propagated and control sounds were made with a Sennheiser ME 67 microphone and a Marantz PMD661 recorder (Marantz, Kanagawa, Japan).

Transmission measurements at the 100 m distance were only obtained for male songs in the forest habitat. Female songs were degraded and attenuated at a level preventing reliable comparison with the control sound when measured at 100 m in any of the habitat types. Some sounds recorded were strongly masked by sounds of other animals and were excluded from the analysis.

Measuring parameters of propagated signals

Signal degradation and attenuation during propagation through the natural environment were determined using the program SIGPRO v3.23 (Pedersen 1998). Transmission parameters were estimated by comparing control sound and propagated sounds according to an established protocol (Dabelsteen et al. 1993; Holland et al. 2001; Balsby et al. 2003). The tested sounds were not masked by transient noise of the same frequency. All recorded sounds were individually filtered in the signal frequency ranges characteristic for a given type of call deduced from the respective spectrogram. The background noise (E_{noise}) was measured immediately before the transmission of each analysed sound. This was done in a place with stationary noise only, so no echo would be detected. The compared control and propagated sounds were aligned in time by maximizing the cross-correlation function between them. The matching of model and observation signals allowed me to determinate the quantification of the signal energy (E_y) and allowed for the

calculation of the signal-to-noise ratio (SNR), the excess attenuation (EA), and the tail to signal ratio (TSR). The signal to noise ratio was calculated as SNR = 10 log ((E_y - E_{noise})/ E_{noise}) (Dabelsteen et al. 1993) and allowed me to get information about the net effect of masking and attenuation of acoustic signals. The excess attenuation was calculated as EA = – 20 log(k) – A (Dabelsteen et al. 1993). EA is a parameter that provides information about the energy loss of an acoustic signal over the values provided by spherical spreading (6 dB per double of the distance), i.e. attenuation (A). EA is a parameter informing about the energy loss of the acoustic signal over the values provided by spherical spreading (6 dB per doubling the distance), i.e. attenuation (A). Ratio k is the ratio of the energy of the model signal and the signal observed at given distance. SNR and EA are usually negatively correlated, and both provide information about the potential transmission range of sounds. The tail to signal ratio was calculated as TSR = 10 log ((E_{tail} − E_{noise})/(E_y− E_{noise})) (Holland et al. 2001). The tail of echoes (E_{tail}) is the character of a gradually disappearing extension of the signal

Statistical approach for testing degradation effects

SNR, EA and TSR were the variables measuring propagation qualities of signals. Due to repeated measurements of sounds being collected from the same individual, this was used as a random factor. Linear mixed models were used to compare the measurements of song degradation between the various vocalisation types at the various distances measured. Using linear mixed models allowed from the control of potential non-independence among vocalisations of the same individual. All statistics were calculated with lmer4 package (Bates et al. 2015) for the R environment (v.3.6.3, R Foundation for Statistical Computing). All *P*-values are two-tailed and means are given with ±SE if not stated otherwise.

Ethical note

To my knowledge, the individuals tested in the experiment reflected the population in a representative way with no potential biases resulting from social background, self-selection, habituation or other factors as indicated in the STRANGE framework (Webster & Rutz 2020). The first part of this study has exclusively observational character, and due to national law for this type of study formal consent is not required (The Act on Experiments on Animals (Disposition no. 289 from 2005). The experimental procedures adhere to the ASAB/ABS (Association for the Study of Animal Behaviour / Animal Behavior Society) Guidelines for the care and use of animals (The Ethics Committee (ASAB) and the Animal Care Committee (ABS), 2019) and was approved by the Local Ethical Committee for Scientific Experiments on Animals (permission no. 16/2015) and the Polish Laboratory Animal Science Association (certificate no. 1952/2015 to Tomasz Osiejuk) conforming to Directive 2010/63/EU.

RESULTS

Natural singing behaviour: microphone array data

Sound material analysed

In total, eight whole day recording sessions were analysed with 1-3 focal pairs recorded simultaneously (N = 18 pairs). This produced nearly 900 hrs of single channel recordings in which 5,934 call and song bouts were detected, these containing a total of 88,442 call and song phrases. Among those bouts, 4,753 (80%) were assigned to the 18 focal pairs, while 1,181 (20%) were considered as being produced by neighbours, from adjacent territories outside the microphone array, based on their appearance on particular channels of the recording.

Types of call and song bouts produced

A majority of 75.4% of all bouts recorded (N = 4,472) were produced by males (63.2%), with a lower amount being produced by females (36.8%). Among the 991 female solo bouts, 16.7% were call bouts or non-song vocalisations. Duet bouts accounted for 24.6% (N = 1,462) of all vocal behaviour detected. The phrases of males and females produced in solos and duets were easy to categorise to a limited number of classes based on audio detection and visual inspection of spectrograms.

Male solos

Male Yellow-breasted boubous of the studied population produced three whistle phrase types: High whee-oo, Low whee-oo and Hwee-hwee (later abbreviated to H, L and W) (Fig. 3.1). Very consistent and statistically significant differences were found when considering the proportions of these three phrase types used by all males as solos (GLMM, $\beta \pm SE = -0.21 \pm 0.014$; $z = -14.75$, $P < 0.001$). The High whee-oo song type was produced the most often 57 ± 2.3 % (95%CI: 52.2-61.4%), then Low whee-oo 28 ± 1.8% (95%CI: 24.3-31.5%), and lastly Hwee-hwee 15 ± 1. 2% (95%CI: 12.8-17.8%).

Female solos

Female vocalisations had a completely different acoustic structure than the whistle type of the male phrases. Female vocal signals were atonal, harsh notes of differing durations. Most of them were classified as Keck (Q, 59.1%), Chock-series (Cs, 32.5%), Chock (C, 3.8%) and Kee-roo (K, 3.5%) with very few examples of Rasp (R, 1.1%) (Fig. 3.2).

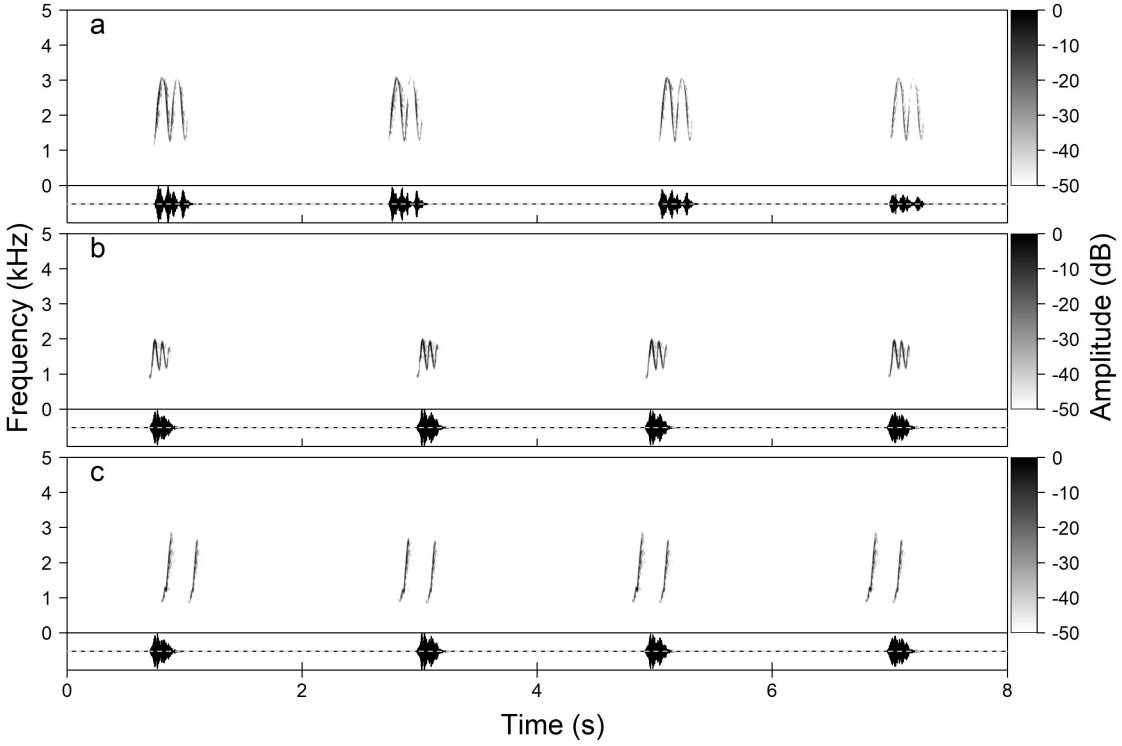

Fig 3.1. Spectrograms of the three different types of male Yellow-breasted boubou vocalisations: (a) High whee-oo (H), (b) Low whee-oo (L) and (c) Hwee-hwee (W). The singing rate is typical for the species.

Kecks were rattle-like calls exclusively produced in a high rate series consisting of up to hundreds of single and very short notes. Visual observations clearly suggest that Kecks were produced in an alarm context, e.g. close to the nest. Chock-series were always produced as a series of 2-14 song phrases with a high rate, almost without gaps between phrases (0.8-0.15 s) and with up to 14 phrases in a row. Chocks had a similar but distinguishably different structure to chock-series, and were produced as a single, double or triple-unit as one phrase after another but without consistent spacing in time, apparently different to the characteristics for the Chock-series. Rasps were very rarely produced (recorded only 33 times) and seem to be produced in the context of high excitation (own unpublished data). Rasps were also relatively quieter in comparison to the other vocalisations, which may on occasion lead to the non-recording of such phrases. Therefore, the Rasp phrase was not included in most of the analyses. Based on both array recordings and observations of vocalising birds it is uncertain as to whether Kecks and Rasps are also produced by males. Unlike males, the proportions of phrase types (Cs, C and K) used for solo singing were very variable (GLMM, $\beta \pm SE = -0.29 \pm 0.054$; $z = -5.44$, $P < 0.001$) among females from the 18 focal pairs. Chock-series were the most commonly observed song type among female solos: 71 ± 8.7% (95%CI: 53.8-88.0%), then Kecks 16.8 ± 8.2% (95%CI: 0.3-33.4%), Kee-roos 12.2 ± 4.3% (95%CI: 3.1-20.7%) and finally Chocks 5.6±2.7% (95%CI: 0.01-10.98%). If I consider female notes classified as functional calls, Kecks were commonly used by all females 98.1 ± 0.01% (95%CI: 96.6-99.7%) while Rasps were found 1.9 ± 0.7% (95%CI: 0.33-3.39%)

incidentally. The basic temporal characteristics of male and female vocalisations are presented in Table 3.1.

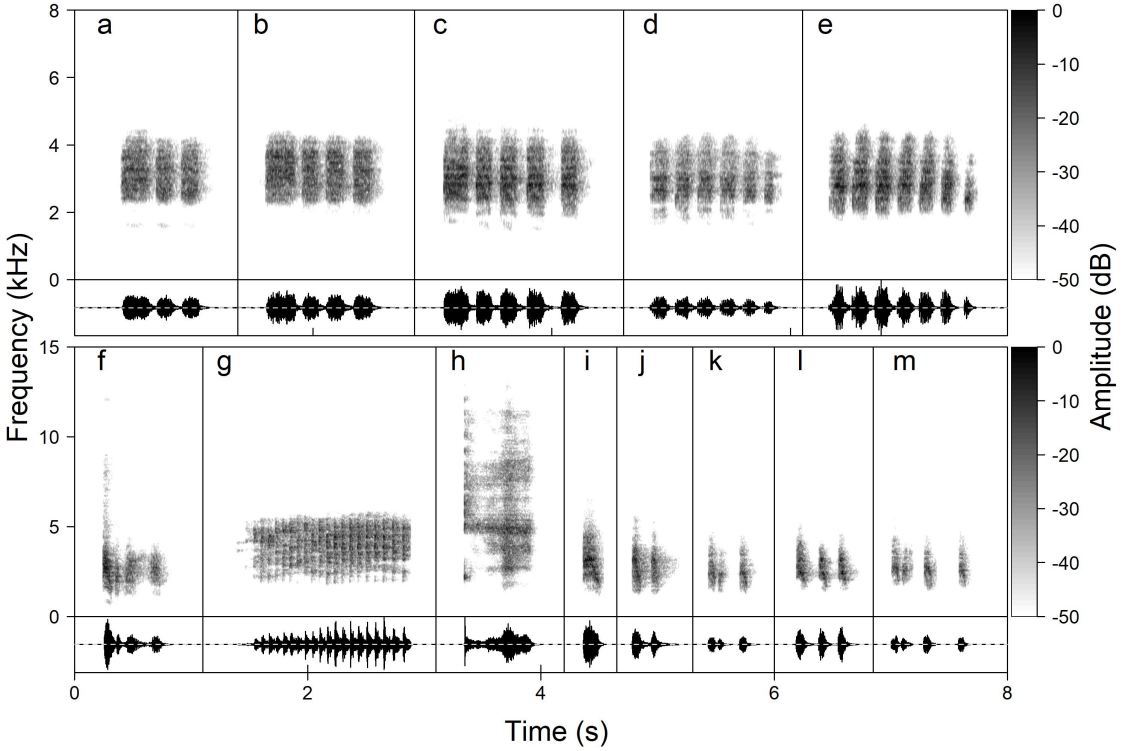

Fig 3.2. Spectrograms showing the variety of female Yellow-breasted boubou songs and calls: (a-e) female Chock series which are always produced in a series, here it is shown in a series of 3 up to 7; (f) Kee-roo song type; (g) Keck alarm call; (h) Rasp excitation call; (i-m) Chock song phrases that are used to lead duets and respond to male songs.

Table 3.1. Temporal characteristics of song phrases and call bouts of Yellow-breasted boubou produced solo by males and females.

Vocalisation	No of units in a bout		Bout duration (s)		Rate (units/min)	
	$\bar{x}$ ± SE	95%CI	$\bar{x}$ ± SE	95%CI	$\bar{x}$ ± SE	95%CI
Male solos						
High whee-oo	8.0±0.20	7.66-8.45	26.0±0.73	24.60-27.49	35.1±0.69	33.72-36.43
Low whee-oo	10.0±0.34	9.31-10.64	31.5±1.17	29.20±33.81	32.5±1.01	30.49-34.44
Hwee-hwee	11.1±0.68	9.81-12.47	31.4±2.04	27.39-35.41	36.9±1.27	34.38-39.38
Female solos						
Chock	6.8±0.59	5.63-8.01	43.6±3.19	37.25-50.02	94.9±43.07	8.80-181.07
Chock-series	5.0±0.07	4.84-5.10	1.9±0.01	1.25-1.31	172.4±18.12	136.82-208.05
Kee-roo	5.7±0.91	3.93-7.57	8.54±2.11	4.33-12.76	114.9±10.31	94.23-135.57
Keck*	28±01.43	25.22-30.86	8.72±0.42	7.89-9.55	232.1±4.28	223.71-240.52
Rasp*	4.4±0.73	2.84-5.89	18.79±6.22	5.71-31.86	64.8±10.28	43.25-86.44

*Keck and Rasp vocalisations were recognized as functional calls (alarm and excitement). See text for details.

Duets

When performing duets, Yellow-breasted boubous use the same phrase types as used for solo vocalisations. Of the 1,462 detected duetting bouts, 85.1% of these were simple duets that consisted of a single male and female phrase type. Male boubous initiated duets most often (81%) and in the cases where females initiated duets (19%) the female would usually revert to following the male song component as seen in male initiated duets. In duet bouts where female phrase contribution is higher than males, female song is still organised in time in relation to the male elements which are produced at a very constant rate.

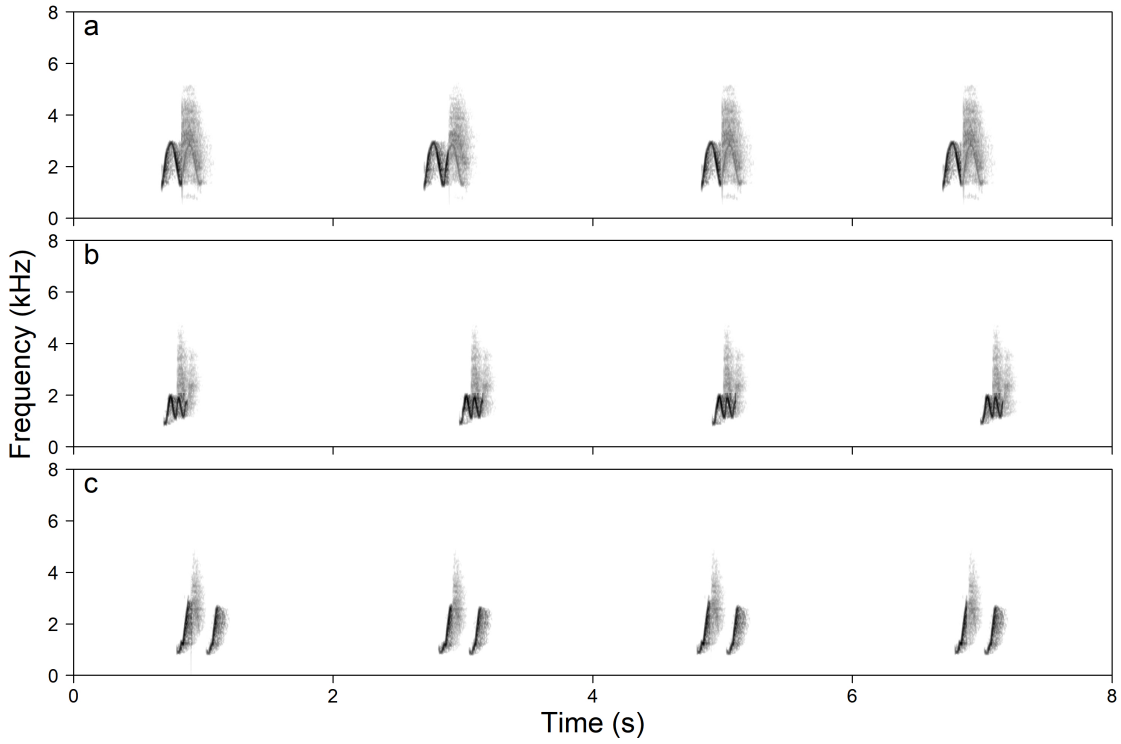

Fig 3.3. Examples of the Yellow-breasted boubou duets: (a) male-initiated and male-led duet_male High whee-oo and female Chock, (b) female-led duet_female Chocks and male Low whee-oo, and (c) female-initiated and female-led duet_triple or double or female Chocks and male Hwee-hwee phrase types. Duetting rate is typical for the species.

The most typical male initiated duets used H phrases (52%) then L (38%) and finally the W phrase type (10%) (Fig. 3.3). Female initiated duets most often used the Cs (42%), K (35%) and C (20%) phrase types. When focusing on the duetting behaviour of the 18 focal pairs, it seems only one duet type, CsHK, was found in the repertoire of all pairs. Other common duet types that were found in 50% of pairs or over include: HK, LK, KL, CsLK, HC, CH, KW. Other types were produced by just under half of the tested pairs (44%), LC,WC,CL,KH. The rest of the duetting sequences were rarely recorded and I found 16 duet types produced only once by a single pair (More details are in Supplement Table S1).

Duet initiation and answering analysis

If it is assumed that every spontaneous song phrase produced by a male or female has been answered by its mate, it can be considered that our results reflect individual decisions (Logue & Krupp 2016). In total, the study species tend to sing more in solos than duets. The three male phrase types remained unanswered by the female in 60.8-79.4% of cases (Table S1). The very common female phrase Chock-series remained unanswered by a mate in 81.9% of cases. The female phrase types Kee-roo and Chock remained unanswered in 37.0% and 53.8% of cases, respectively. A completely different pattern was found for Keck calls as they were almost never answered (99.8%) by males. The Rasp calls were also rarely answered by males (76.0%), but they were also very rarely recorded. This suggest that both Kecks and Rasps are not produced by females to form duets, but just when females are alarming (Kecks) or are highly excited (Rasps), males may also produce song phrases, but not in a coordinated way with the female (Table S1).

Temporal characteristics of male and female solos

Male solo bouts produced phrases with surprisingly similar average rates (Table 3.1) which did not differ significantly between phrase types (GLMM, $\beta \pm SE = 0.02 \pm 0.795$, $z = 0.03$, $P = 0.976$). On the other hand, the differences in the number of phrases within a bout (GLMM, $\beta \pm SE = 0.07 \pm 0.012$, $z = 5.92$, $P < 0.001$) and as a consequence the bout duration (GLMM, $\beta \pm SE = 0.05 \pm 0.015$, $z = 3.62$, $P < 0.001$) were significantly different between bouts produced with different phrase types (with the following pattern H > L > W). Thus, males produced solos with a very regular and fixed rate, but obviously changed bout duration by producing more or fewer phrases in a series. I did not record male solo bouts with more than a single phrase type.

A different situation was found for females (Table 3.1). As was mentioned already, three types of vocalisations (Chock-series, Chocks and Kee-roos) were used by females as songs, while the remaining two were used as calls (Kecks and Rasp). In the majority of cases the Chock-series remained unanswered by males and they were never repeated one after another. Chocks and Kee-roos produced as a solo had similar temporal organisation, typically with 4-8 notes in a bout and they were used both to initiate duets and as a response to males during duets. Female solo song bouts of different types (Chock-series, Chocks and Kee-roos) significantly differed in number of phrases (GLMM, $\beta \pm SE = 1.04 \pm 0.204$, $z = 5.07$, $P < 0.001$), duration (GLMM, $\beta \pm SE = 2.81 \pm 0.192$, $z = 14.63$, $P < 0.001$) and song rate (GLMM, $\beta \pm SE = -76.21 \pm 3.901$, $z = -19.53$, $P < 0.001$). Keck calls were clearly different from other vocalisations, as they were produced with extremely high rates and sometimes in a very long series. Rasps were recorded rarely, hence it is

hard to temporally characterise them in more detail. However, recorded examples indicate a sudden and irregular appearance.

Temporal characteristics of duets

On average, birds used 22.3 ± 0.63 (95%CI: 21.1-23.5) phrases in a duet, and the average duet duration was 30.3 ± 0.89 s (95%CI: 28.5-32.0). The rate of duet phrases doubled those of solos, with an average of 68.0±1.27 phrases per minute (95%CI: 65.5-70.5). Duets initiated by males were longer (on average 32.0 vs 24.7 s; GLMM, β ± SE = 4.81 ± 2.042, z = 2.35, P = 0.019), but contained fewer phrases (21.4 vs 25.1; GLMM, β ± SE = -3.57 ± 1.721, z = -2.07, P = 0.038) and had a lower rate (62.5 vs 94.6 phrases/min; GLMM, β ± SE = -29.22 ± 3.229, z = -9.05, P < 0.001) than female initiated duets.

I found significant differences in the number of the male and the female phrases in duets initiated by male and female (GLMM, β ± SE = -1.75 ± 0.114, z = -15.41, P < 0.001). If duets were initiated by males, the number of male and female phrases within a duet was almost equal (Sex bias = 0.98 ± 0.014, 95%CI: 0.95-1.01).

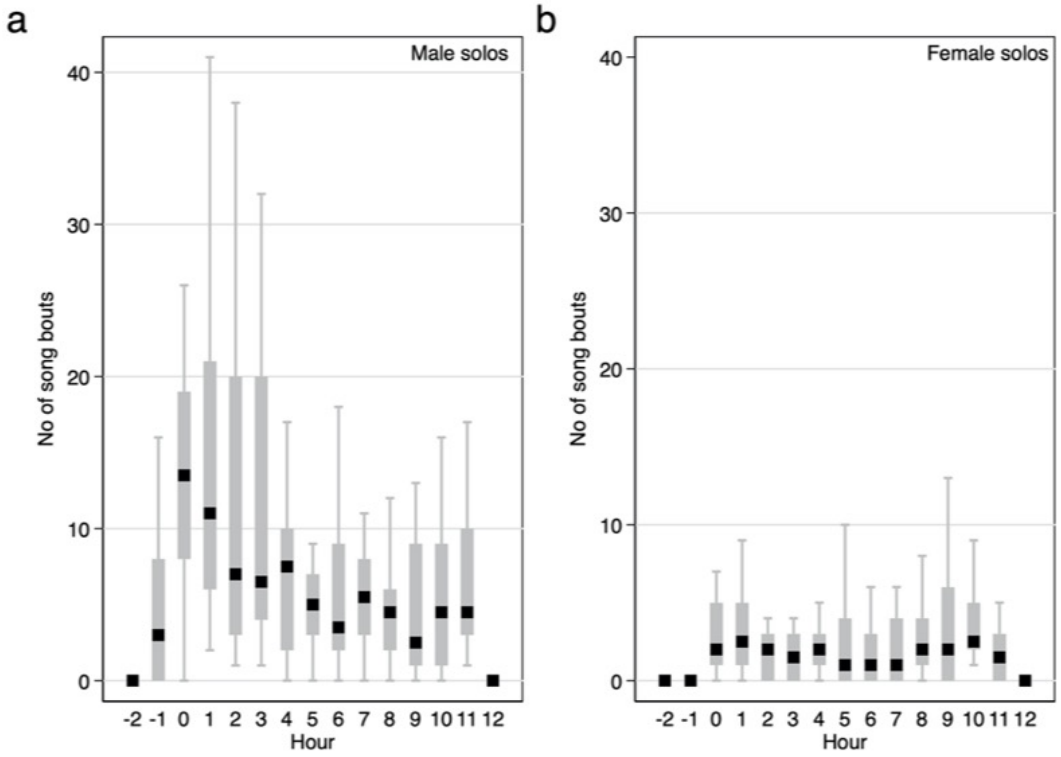

Fig 3.4. Number of solo song bouts of (a) males and (b) females per hour/ per pair. The boxes indicate the 25th – 75th percentile and lower-upper adjacent values. Only data for the 18 tested pairs of Yellow-breasted boubou were included here.

However, if females were initiating duets, they produced significantly more phrases than males (Sex bias = 2.67 ± 0.206, 95%CI: 2.27-3.08). Characteristically, males responded to females initiating duets with any type of their song phrase repertoire (Table S1). If a female initiated the duet with a Chock-series she always switched later in a bout to Chock or Kee-roo phrases. Consequently, Chock-series were never used within a duet and never repeated one after another.

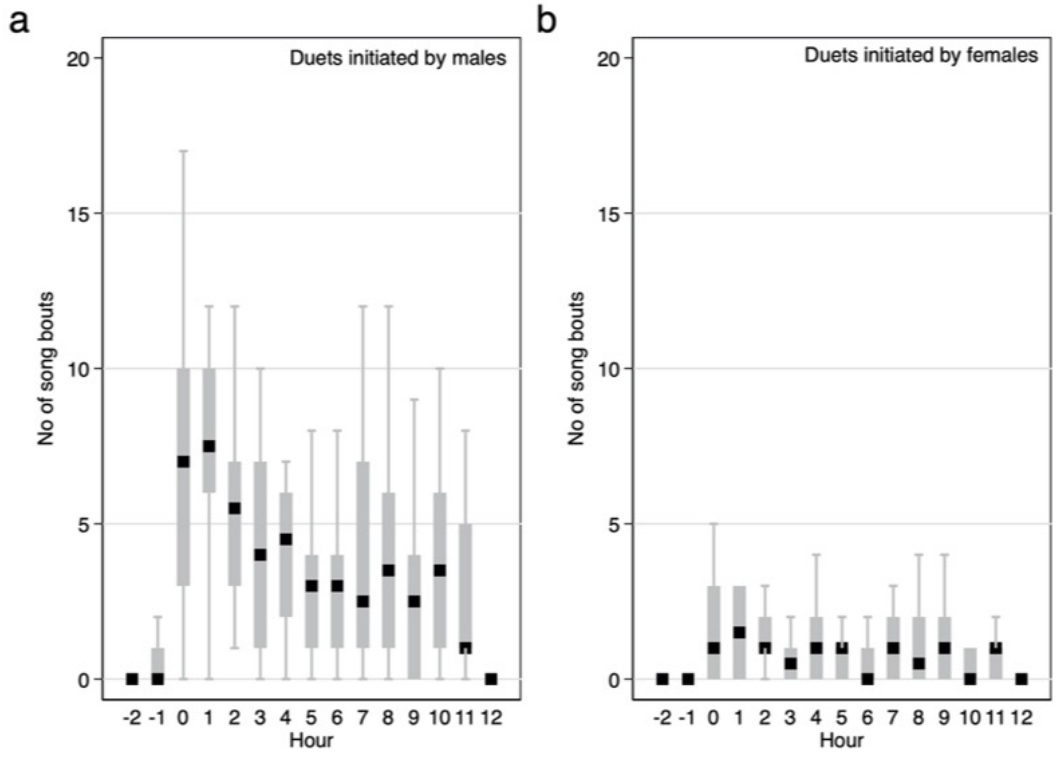

Fig 3.5. Number of (a) male and (b) female initiated duets per hour/ per pair. Boxes indicate the 25th – 75th percentile and lower-upper adjacent values. Only data for the 18 tested Yellow-breasted boubou pairs were included here.

Diurnal pattern of vocal activity during breeding season

I found that Yellow-breasted boubous started to vocalise on average 16 ± 6.1 mins before sunrise (95%CI: 30.0-3.3 mins before sunrise; extremes from 61.1 mins before to 23.7 mins after sunrise) and that singing activity was the highest during the first two hours after sunrise (Figs. 3.4 and 3.5). Interestingly, birds were vocally active during the whole day, even between 11:00 and 15:00 when the temperature was usually quite high (24.8-31.0°C) in comparison to dawn (14.5-16.4°C; more details in Szymański et al. 2021). Characteristically, the number of bouts per hour in which females were involved were small (Figs. 3.4 & 3.5), and there were no significant trends for number of female solos produced during the daytime (GLMM, β ± SE = 0.07 ± 0.047, z = 1.54, P = 0.124) and duet bouts initiated by females (GLMM, β ± SE = -0.02 ± 0.019, z = -0.85, P = 0.393). Thus, the main part of the overall variability of the singing activity during the day resulted

from the activity of male solos and duets initiated by males (Figs. 3.4 and 3.5). The number of male song bouts significantly decreased during the day time (GLMM, $\beta \pm SE = -0.32 \pm 0.107$, $z = -2.95$, $P = 0.003$), although male initiated duets did not differ significantly throughout the day (GLMM, $\beta \pm SE = -0.10 \pm 0.057$, $z = -1.78$, $P = 0.075$).

I analysed who, and with what song type, first started vocalising in the morning. When the 18 focal pairs were analysed, 78% of cases started with a male solo bout (and 9 of these 14 cases were males singing with the W phrase type). Duets were observed as the first song bout in two pairs (11%; KL and HK) as were female solos (two cases, 11% of Q). A long series of Kecks (Q) given by females were observed as an apparent response to a threat (human or squirrels close to nest) and so these two early cases of Kecks given by females might be interpreted as an unspontaneous dawn chorus but are more likely used as a response to a predator.

Experiments E1 and E2: Intrusion of male solos, female solos and duets

Response to duet and solo stimuli

I conducted experiments with 36 different pairs, 18 tested with a single speaker (E1) and 18 with double speakers (E2). Each pair was tested three times, giving a total of (2 experiments × 3 treatments × 18 pairs) 108 trials with 36 different individuals. The majority of the tested Yellow-breasted Boubous responded to simulated intrusion with all three kinds of playback. However, in 11 cases in E1 (20%) and in 5 cases in E2 (9%), approaching or vocal responses were observed (Fisher exact test $P = 0.1744$). Birds responded in 1 of 3 ways, they either only vocalised, only approached or responded by vocalising and approaching together, the latter response was the most often demonstrated (57% in E1 and 69% in E2; for details see Table 3.2). Birds did not respond, in significantly ($\chi^2 = 7.190$, $P = 0.027$) more cases, when tested with female solo playback (10 trials), than when responding to male solo and duet playback (3 trials in each treatment; details in Table 3.2).

Table 3.2. Summary of responses to playback of female solo, male solo and duet playbacks in single speaker and double speaker experiments.

Categories of response to playback	Single speaker experiment			Double speaker experiment		
	Female solo	Male solo	Duet	Female solo	Male solo	Duet
No response	7	2	2	3	1	1
Vocal response (only)	3	3	3	2	2	1
Approaching (only)	1	0	2	2	3	2
Approaching and vocal response	7	13	11	11	12	14

Characteristics of response to duet and solos

The strong response of birds was linked with fast approaching to the speaker(s) and intensive duetting led by males that was reflected by the lower PC1 scores. There was a significant effect of the Treatment (GEE, Wald χ^2 = 16.00, $P < 0.001$) and Treatment×Experiment interaction (GEE, Wald $\chi^2 = 8.64$, $P = 0.013$; Table 3.4). The differences found were largely the effect of (i) weaker responses to female solo than to male solo and duets, and (ii) stronger responses to duets played back from two speakers in E2, in comparison to duets played back from a single speaker in E1 (Table 3.3, Fig. 3.6).

Table 3.3. GEE on factors affecting Yellow-breasted boubous response measured by PC1 - Approaching and duetting and estimates of parameters associated with birds' responses. The best model presented with QIC/QICC equal 96.918.

Factors	Wald χ^2	df	*P*
Intercept	0.00	1	1
Experiment	3.58	1	0.058
Treatment	16.00	2	**<0.001**
Experiment×Treatment	8.64	2	**0.013**
	Coefficient estimate	Standard error	*P*
Intercept	-0.74	0.223	0.001
Experiment: Single speaker	0.89	0.313	**0.004**
Experiment: Double speaker	0[a]		
Treatment: Female solo	1.03	0.236	**<0.001**
Treatment: Male solo	0.70	0.295	**0.017**
Treatment: Duet	0[a]		

Significant *P* values are indicated in bold.

[a]Baseline categories of the categorical variable; *p* values pertain to the significance of estimates (slopes of covariates of differences between subsets of categorical variables).

Yellow-breasted boubous stimulated by the two speakers stayed closer to one of the speakers ($\bar{x}$±SE = 9.5 ± 2.63 m), than when they were stimulated with a single speaker only ($\bar{x}$±SE = 21.8 ± 4.92 m). Such a response was also linked with more flights during the duet treatment in E2 ($\bar{x}$±SE = 4.9 ± 0.59) in comparison to E1 ($\bar{x}$±SE = 2.7 ± 0.51). Additionally, the vocal response was stronger to duets presented from two speakers. The number of phrases sung in male initiated duets in E2 ($\bar{x}$±SE = 56.9 ± 14.17) was over three times larger than in E1 ($\bar{x}$±SE = 16.8 ± 5.35).

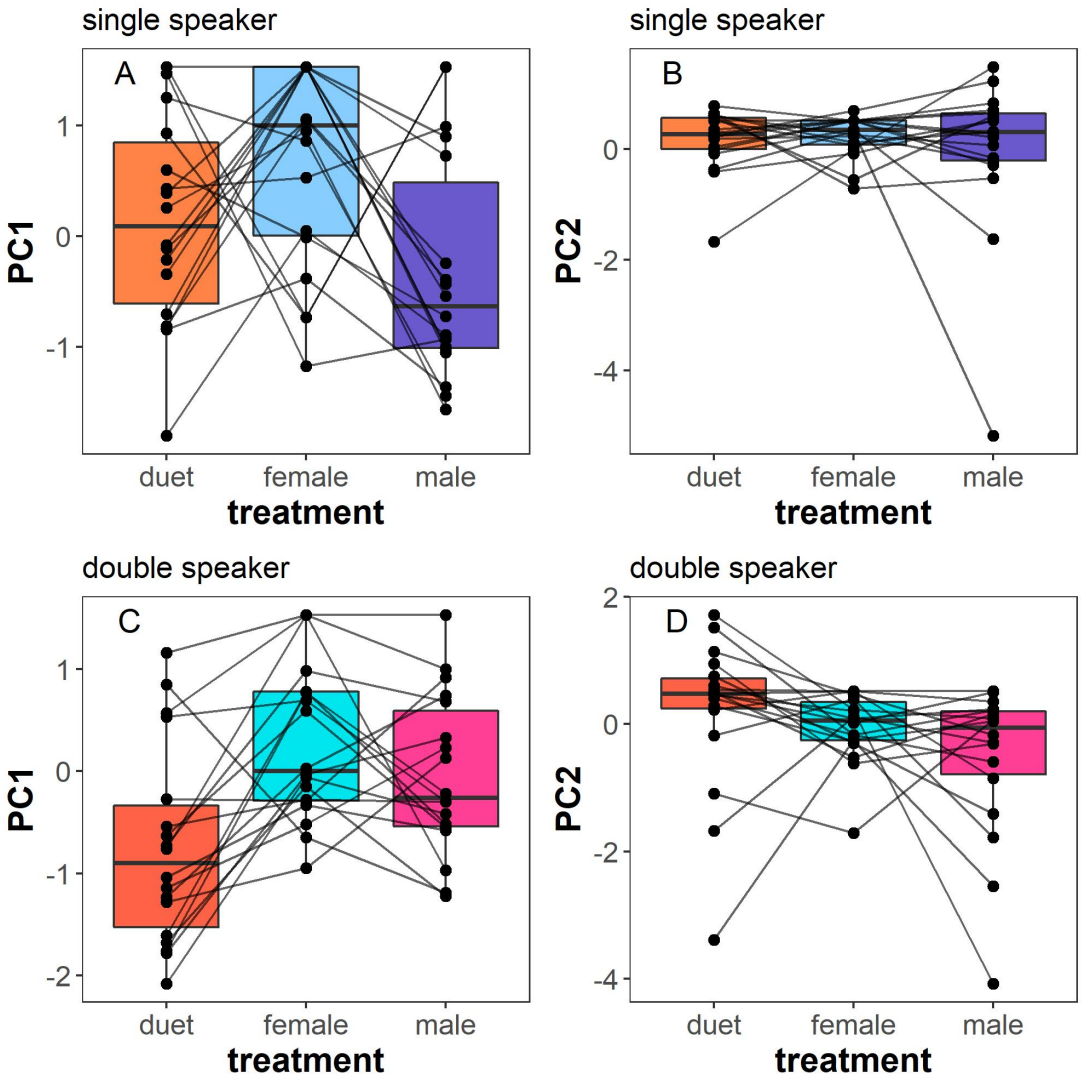

Fig 3.6. The responses by Yellow-breasted boubous to female solos, male solos and duets to single speaker (A-B) and double speaker (C-D) experiments. PC1 represents approaching and duet components of the study species behavioural response whereas PC2 represents male solo components. For both PC1 and PC2 the lower values indicated a stronger response. Box plots indicate medians and interquartile ranges. Individual values for each tested pair are linked with lines.

The PC2 component was strongly related to a single original response measure, namely male solos (Table 3.4). There was no significant effect of the experiment or treatment, on this component, including the interaction between these two variables (all $P > 0.16$; Table 3.4; Fig. 3.6). Males produced solos in response irrespective of the closest distance to the speaker they reached and without any clear relation to the other response measures.

For the duet treatment in E2, where male and female speakers were separated by a 10 m distance, I found that at the start of the playback females came closer to the female speaker in 12 cases (binomial test $P = 0.238$) and males to a male speaker in 9 cases (binomial test $P = 0.814$). However, during the experiments progression they usually did flights or small jumps and changed

positions. I found that despite the use of two speakers it was hard to measure quantitatively measure the differences in response of a particular sex to a particular speaker as both birds were involved in a similar way.

Table 3.4. GEE on factors affecting Yellow-breasted boubous response measured by PC2 - Male solos and estimates of parameters associated with birds' responses. *The best model presented with QIC/QICC* equal 111.194.

Factors	Wald χ^2	df	*P*
Intercept	0.00	1	1
Experiment	1.92	1	0.165
Treatment	3.26	2	0.195
Experiment×Treatment	1.43	2	0.489
	Coefficient estimate	Standard error	*P*
Intercept	0.21	0.276	0.576
Experiment: Single speaker	-0.04	0.306	0.904
Experiment: Double speaker	0[a]		
Treatment: Female solo	0.33	0.315	0.296
Treatment: Male solo	0.55	0.539	0.304
Treatment: Duet	0[a]		

Significant *P* values are indicated in bold.

[a]Baseline categories of the categorical variable; *P* values pertain to the significance of estimates (slopes of covariates of differences between subsets of categorical variables).

Sex bias

By only considering experiments with strong male or female bias in response to both experiments, there was no significant difference in response to the different treatments ($\chi^2 = 3.62$, $P = 0.163$). On the other hand, if I looked at the experiments in which birds only responded vocally with male led duets and demonstrated no sex bias in approaching behaviour, the situation changes. By treating these cases as male biased responses shows know significant difference between treatments ($\chi^2 = 5.22$, $P = 0.461$), however if they are categorised as not having sex biased responses a significant difference is apparent ($\chi^2 = 9.77$, $P = 0.044$). This being an effect of having three times more female-biased responses ($N = 15$) than male biased responses ($N = 5$) to duets. I found a clear pattern among both experiments and all treatments, that if response was characterised by stronger investments of females than males (more female phrases, closer approaching), the general response as measured by PC1 was significantly stronger (GEE, Wald $\chi^2 = 113.74$, $P < 0.001$).

Experiment E3: Intrusion of duets with different male song components

The responses of 18 pairs were tested and analysed, each pair being tested three times with three different duet types (HC, LC and WC, total $N = 54$ experiments). I found that in 36 of the

experiments (66.7%) pairs responded to playback with duets, in 13 experiments (24.1%) males produced solos, and in 10 experiments (18.5%) females sang solos. However, in only six experiments solos were the only vocal response that were produced (four male solos and two experiments for females). Approaching of males was observed in 44 experiments (81.2%) and in 41 experiments (75.9%) for females. Males approached within a 10 m distance to the speakers in 25 experiments (46.3%) and females in 24 experiments (44.4%). I found no statistically significant differences in distribution of all the above binary responses between treatments as well as between sexes within response category (all $P > 0.197$ for χ^2 or Yates' χ^2 tests).

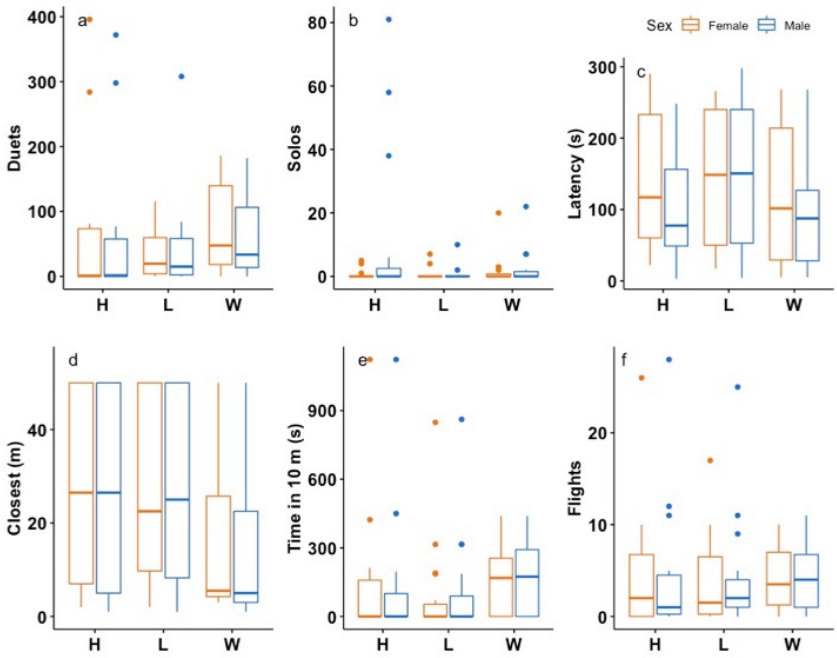

Fig 3.7. Female and male responses to playback of different duet types (H, L, and W indicate duets with different male component and the same female Chock component): (a) number of phrases produced in duets, (b) number of phrases produced solo, (c) latency to respond (s), (d) closest distance of approach to speaker (m), (e) time spent in a distance within 10 m to speaker (s), (f) number of flights to speakers. Box plots show the median with a horizontal line, the interquartile range (25th–75th percentile) with boxes, and the values within 1.5 times the interquartile range with whiskers. Dots show values exceeding 1.5 times the interquartile range.

Quantitative measures of response and relevant tests are presented in Fig. 3.7 and Tables 3.5-3.6. The general rule observed was that the male and female of a focal pair were responding together and in a coordinated way. Consequently, male and female measures of response within a particular response category were highly correlated, and I did not observe significant sexual bias in the response, including in the response to different playback types (Tables 3.5 and 3.6). A significant effect of the order of experiment ($P < 0.001$) and treatment ($P = 0.007$) on the number of song phrases produced by males and females in duets was found (Table 3.5). Pairs produced significantly more phrases in duets in the first (post hoc $P = 0.043$) than in the following

two experiments with same pair (mean duet phrases±SE for experiment order: 1st: 84.4 ± 16.80, 2nd: 50.7 ± 11.96, 3rd: 27.4 ± 7.63). As for the effect of treatments, the strongest duetting response was toward the WC playback (68.1 ± 10.67), then to the HC playback (55.1 ± 17.74), and finally to the LC playback (39.4 ± 9.48) (Fig. 3.7). Solo responses to playback were relatively rare (see above) and when this happened, birds never produced as many phrases as duets. The only significant effect was found for the Treatment×Order interaction (Table 3.5), which was the result of many more solos (15.5 ± 8.03) produced when birds responded for the first time to the HC treatment. However, this was only observed in a few experiments and usually males produced less solos (2.7 ± 1.01).

Table 3.5. Factors and interaction terms from the generalized linear mixed models used to analyse vocal responses of the yellow-breasted boubou to playbacks simulating intrusion of a stranger pair singing three different duet types.

	Number of song phrases produced in duets			Number of song phrases produced solo		
	F	df	*P*	*F*	df	*P*
Treatment	5.30	2,94	**0.007**	1.96	2,94	0.146
Order	9.89	2,94	**0.000**	1.93	2,94	0.151
Sex	0.09	1,94	0.770	2.58	1,94	0.112
Treatment × Order	2.20	4,94	0.075	3.24	4,94	**0.015**
Treatment × Sex	0.03	2,94	0.974	1.74	2,94	0.181
Order × Sex	0.02	2,94	0.981	1.41	2,94	0.249

Table 3.6. Factors and interaction terms from the generalized linear mixed models used to analyze four aspects of approaching behavior responses of the yellow-breasted boubou to playbacks simulating intrusion of a stranger pair singing three different duet types.

	Latency to approach speaker (s)			Closest approach to the speaker (m)			Time spent within 10 m to speaker			Number of flights		
	F	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Treatment	2.46	2,94	0.090	4.93	2,94	**0.009**	6.22	2,94	**0.003**	1.58	2,94	0.213
Order	5.93	2,94	**0.004**	4.00	2,94	**0.022**	3.77	2,94	**0.027**	8.08	2,94	**0.001**
Sex	0.98	1,94	0.325	0.34	1,94	0.562	0.15	1,94	0.696	0.01	1,94	0.906
Treatment × Order	1.16	4,94	0.334	0.96	4,94	0.433	1.06	4,94	0.380	3.66	4,94	**0.008**
Treatment × Sex	0.19	2.94	0.824	0.00	2,94	0.997	0.03	2,94	0.971	0.19	2,94	0.830
Order × Sex	0.29	2,94	0.749	0.00	2,94	0.996	0.04	2,94	0.964	0.02	2,94	0.981

The approaching behaviour was described by four variables which, although correlated with each other, describe slightly different aspects of this behaviour. All approaching variables (Table 3.6) were significantly affected by the order of experiment. Birds were less likely to approach quickly and closer when they were tested once again (all *P* between 0.001-0.027). There was also a significant effect of treatment on the closest distance to the speaker ($P = 0.009$) and time spent within 10 m to the speaker ($P = 0.003$). Birds came closer to the speaker when I played back the WC duets (16.3 ± 3.20 m) than the HC (27.1 ± 3.43 m) and the LC (27.5 ± 3.26 m) duets. Tested pairs spent significantly more time within a 10 m radius, when responding to the WC duet (161.3 ± 24.79 s), than to the HC (124.8 ± 45.18 s) and the LC (94.7 ± 35.23 s) duets. In general, I did

not observe significant differences in flight numbers between treatments. However, a significant effect of the Treatment×Order interaction on flight numbers was found ($P = 0.008$). As with the case of solos, birds did many more flights (9.7 ± 2.58) when responding for the first time to the HC treatment (the general mean of flights per individual in all experiments was only 4.2 ± 0.51).

Matching

I found that males matched the male-part of duets provided by in only 14 experiments, which means 25.9% of all experiments or 35.0% of experiments in which males sang any song in response. The latter value is thus very close and not significantly different from the predicted random pattern of matching ($\chi^2 = 0.07$, df = 1, $P = 0.92$). In this study males matched the HC playback 2 times, the LC playback 3 times, and the WC playback 9 times, which gives 11.1%, 16.7% and 50% of particular song type matching. Whichever way you look at this data (natural solos frequency perspective: Yates' $\chi^2 = 26.39$, df = 2, $P < 0.001$; duets perspective: Yates' $\chi^2 = 41.89$, df = 2, $P < 0.001$), it shows that males have avoided matching the most commonly used H type, as well as the L type, which, in turn, is comparably more often used in duets (though less in solos). On the other hand they matched, more often than expected by chance, the WC playback. This result was also confirmed by the GLMM with matching behavior included as a binary response variable and treatment as an independent factor ($F = 3.69$, df = 2,51, $P < 0.032$). Moreover, pairs in which males matched the playback responded significantly stronger in all response variables. Such pairs produced more duets (Fig. 3.8a) and solos (Fig. 3.8b), as well as approached speakers faster, closer and stayed close for a longer time (Fig. 3.8c-f). Adding matching as an additional factor to GLMM models presented in Tables 3.5-3.6 makes it the strongest predictor of response strength (all P between 0.038 and < 0.001) and in all cases cancels the significant effect of the treatment (all $P \geq 0.098$).

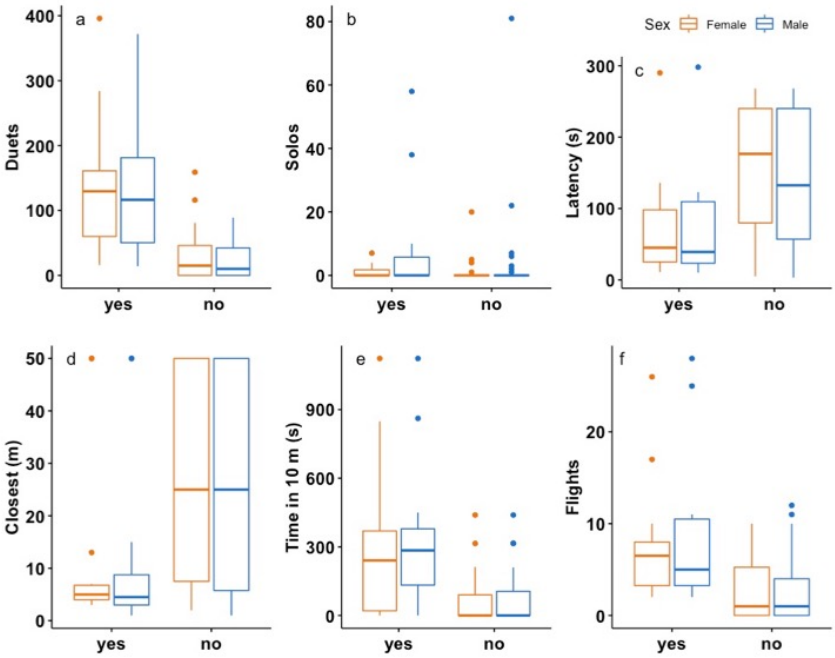

Fig 3.8. Female and male responses to playback in experiments during which focal males matched (*N* = 14) or did not match (*N* = 40) the song type of playback: (a) number of phrases produced in duets, (b) number of phrases produced solo, (c) latency to respond (s), (d) closest distance of approach to speaker (m), (e) time spent in a distance within 10 m to speaker (s), (f) number of flights to speakers. Box plots show the median with a horizontal line, the interquartile range (25th–75th percentile) with boxes, and the values within 1.5 times the interquartile range with whiskers. Dots show values exceeding 1.5 times the interquartile range.

Experiment E4: Propagation of vocalisations through the environment

Differences in song propagation between habitats

Male and female songs degrade significantly differently with both distance and in different habitat types (Fig. 3.9; Tables 3.7–3.9). In the forest locations the transmitted signals were able to be measured up to 100 m from the loudspeaker (source). However, in both the shrub and stream habitat locations this was not possible as the signals were too degraded after reaching the 100 m distance (Fig. 3.10). Yellow-breasted boubou songs propagated significantly worse in the shrub habitat type in comparison to the level terrain of the forest. This was the case for every distance measured (Fig. 3.10).

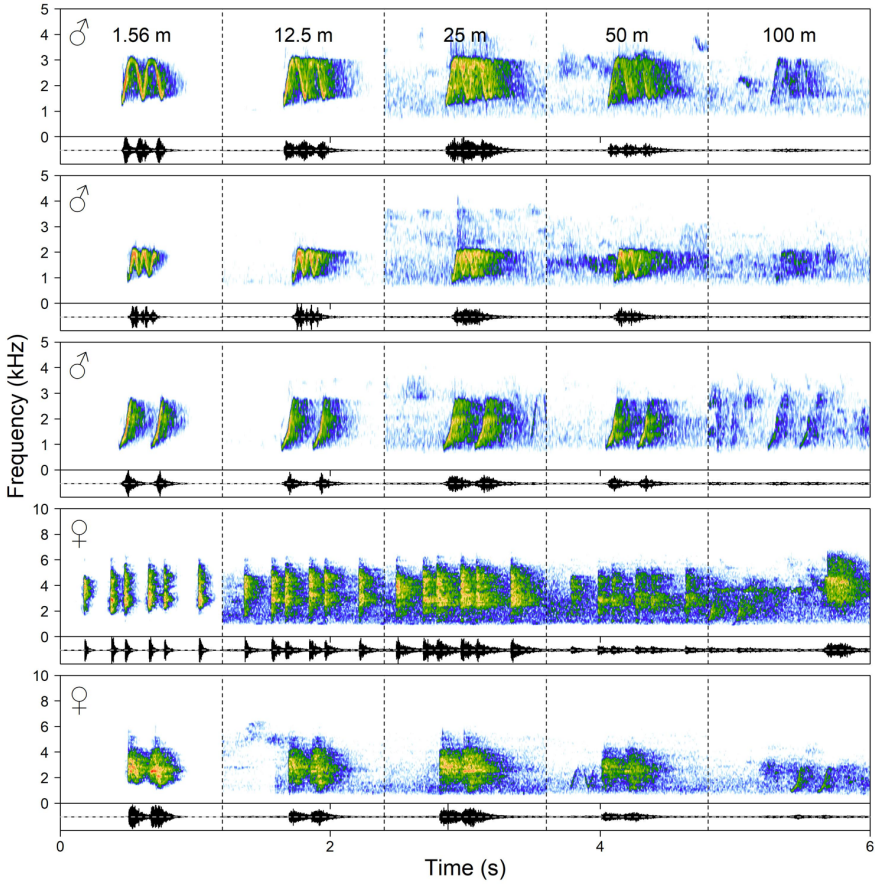

Fig 3.9. Songs and calls before and after propagation. Measurements signals travelled and were recorder ranged from 1.56, 12.5, 25, 50 and 100 m. The first three rows represent male song types and the final two represent female vocalisations.

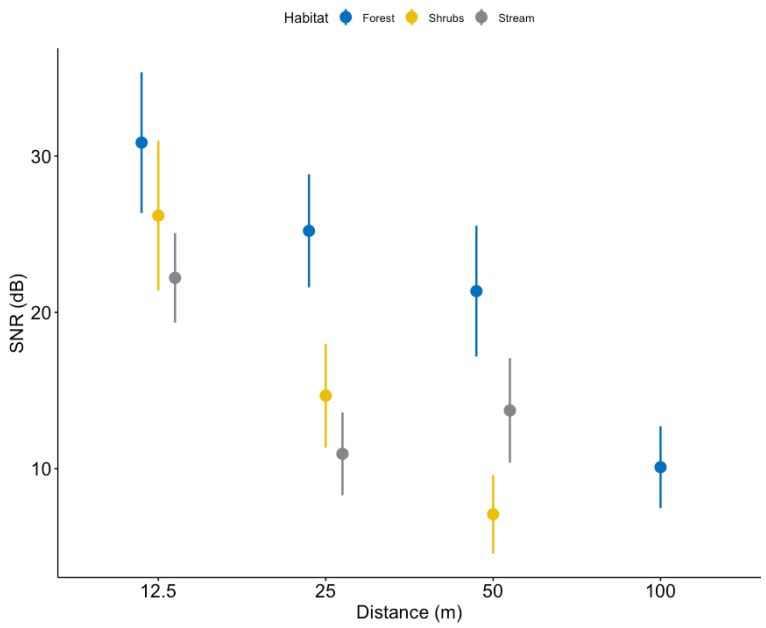

Fig 3.10. SNR for combined male and female song phrases in the forest, shrubs and along the stream. Acoustic signals transmit better in the forest habitat for all distances measured.

Table 3.7. Result of the general linear mixed model for signal-to-noise ratio (SNR) of propagated songs of the Yellow breasted boubou (*Laniarius atroflavus*). Main and two-factor interactions effects are presented for the following source of variation: sex (male, female), habitat (transect FOREST, SHRUBS, STREAM) and distance (12.5, 25, 50 and 100 m).

Source of variation	Coef.	Std. Err.	*t*	*P*
Main effects				
Sex	8.31	1.320	6.29	**< 0.0001**
Habitat	-5.70	0.357	-15.97	**< 0.0001**
Distance	-7.14	0.361	-19.78	**< 0.0001**
Two-factor interaction effects				
Sex × Habitat	-0.76	0.312	-2.45	**0.0145**
Sex × Distance	-0.43	0.323	-1.28	0.2008
Habitat × Distance	0.66	0.098	6.78	**< 0.0001**

Table 3.8. Result of the general linear mixed model for excess attenuation (EA) of propagated songs of the Yellow breasted boubou (*Laniarius atroflavus*). Main and two-factor interactions effects are presented for the following source of variation: sex (male, female), habitat (transect FOREST, SHRUBS, STREAM) and distance (12.5, 25, 50 and 100 m).

Source of variation	Coef.	Std. Err.	t	P
Main effects				
Sex	-14.16	3.458	-4.09	**< 0.0001**
Habitat	4.05	1.120	3.35	**0.0008**
Distance	3.41	1.230	2.77	**0.0055**
Two-factor interaction effects				
Sex × Habitat	1.63	1.052	1.55	0.1215
Sex × Distance	1.66	1.102	1.51	0.1321
Habitat × Distance	-1.22	0.334	-3.66	**0.0002**

Table 3.9. Result of the general linear mixed model for tail-to-signal ratio (TSR) of propagated songs of the Yellow breasted boubou (*Laniarius atroflavus*). Main and two-factor interactions effects are presented for the following source of variation: sex (male, female), habitat (transect FOREST, SHRUBS, STREAM) and distance (12.5, 25, 50 and 100 m).

Source of variation	Coef.	Std. Err.	t	P
Main effects				
Sex	-4.03	0.872	-4.63	**< 0.0001**
Habitat	-0.84	0.225	-3.75	**0.0002**
Distance	2.72	0.227	11.95	**< 0.0001**
Two-factor interaction effects				
Sex × Habitat	0.50	0.196	2.53	**0.0113**
Sex × Distance	-0.06	0.203	-0.31	0.7562
Habitat × Distance	-0.20	0.061	-3.32	**0.0009**

The SNR was ~5 dB lower in the shrub than in the forest, even at a distance as close as 12.5m to the source. This discrepancy increased to ~14 dB at 50m where it was still possible to measure degradation of the songs transmitted in both habitats. When assessing the stream transmission an irregular degradation pattern was found. The SNR was on average larger after 50 m and for the 25 m distance and in both cases SNR values were more similar to the transmission in the shrub location than the forest (Fig. 3.10). There was a significant effect of Sex × Habitat as well as Habitat × Distance interactions on SNR (Table 3.7). This indicates that female songs degraded faster than male songs at the various distances measured as well as in the shrub and stream locations compared to the forest terrain. As expected, the changes in EA with the increased propagation distances revealed a negative correlation pattern when compared to SNR (Table 3.7-3.8). However, the differences in EA between male and female songs were clearly larger than the SNR measurements. The energy loss measured by EA was more substantial in the shrub location than the forest habitat, resulting in a significant effect of the Habitat × Distance interaction. The energy loss of the transmitted songs was larger for female and for the sounds propagated in dense shrub. In addition to these propagation parameters, the sound assessed by the TSR was most strongly affected by the distance, with the significant differences between sexes and habitats still existed (Table 3.9).

Degradation of different vocalisation types

Male and female songs in different habitats

To look further into song propagation of the Yellow-breasted boubou I compared male and female songs within the different habitat types. The sex differences seem to be consistent with all three of the male whistle song types transmitting better than the female songs (Tables 3.10, Fig. 3.11). Differences in propagation parameters were relatively small for male song types compared to female song types when song were transmitted in the forest habitat (Fig. 3.11). For example, the SNR of all three male song types was still around 10-12 dB when being recorded

at 100 m, compared to only 2 dB for females at this distance. In the shrub habitat type, the male and female song types degraded in a more similar way. All female songs degraded more than the male song types in this habitat, but the W male song type was only slightly better at propagation than the female songs (Fig. 3.11). When songs were transmitted in the hilly, stream habitat, male songs once again propagated better than female songs. Female songs were quickly distorted in this habitat type, even as close as 25 m from the source speaker. In general, the decrease in SNR between 12.5 m and 25 m was the most substantial for the stream experiment locations (Fig. 3.11).

Table 3.10. Result of the general linear mixed model for signal-to-noise ratio (SNR), excess attenuation (EA), tail to signal ration (TSR) of propagated songs and alarm calls of the female Yellow-breasted boubou (*Laniarius atroflavus*). Main and two-factor interaction effects are presented for the following source of variation: Vocalisation type (song vs. alarm call of female), Habitat (FOREST, SHRUBS, STREAM), Distance (12.5 m, 25 m, 50 m, 100 m).

Source of variation	Coef.	Std. Err.	*t*	*P*
	SNR (dB)			
Main effects				
Vocalisation type	-6.52	1.134	-5.75	**<0.0001**
Habitat	-14.06	1.517	-9.26	**<0.0001**
Distance	-10.97	1.568	-6.70	**<0.0001**
Two-factor interaction effects				
Vocalisation type × Habitat	2.36	0.323	7.30	**<0.0001**
Type × Distance	1.28	0.333	3.84	**0.0001**
Habitat × Distance	0.06	0.184	0.30	0.7603
	EA (dB)			
Main effects				
Vocalisation type	3.01	2.385	1.26	0.2083
Habitat	10.86	3.401	3.19	**0.0015**
Distance	7.01	3.550	1.97	**0.0451**
Two-factor interaction effects				
Vocalisation type × Habitat	-1.80	0.723	-2.49	**0.0132**
Type × Distance	-1.02	0.753	-1.36	0.1743
Habitat × Distance	-0.99	0.416	-2.38	**0.0175**
	TSR (dB)			
Main effects				
Vocalisation type	1.59	1.151	1.38	0.1678
Habitat	-0.96	1.610	-0.59	0.5527
Distance	5.13	1.666	3.08	**0.0022**
Two-factor interaction effects				
Vocalisation type × Habitat	0.28	0.342	0.83	0.4064
Type × Distance	-0.35	0.353	-0.98	0.3272
Habitat × Distance	-0.73	0.196	-3.73	**0.0002**

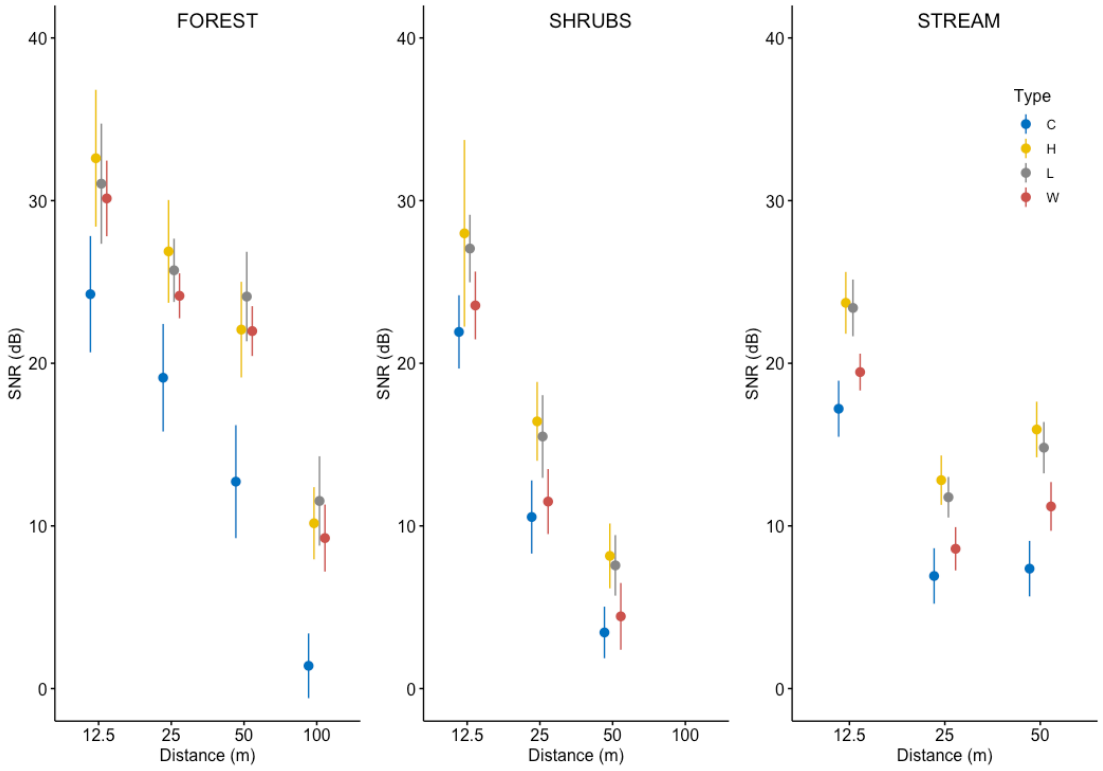

Fig 3.11. SNR for male (H – High whee-oo, L – Low whee-oo, W – Hwee-hwee) and female (C - Chock) song types in the shrub habitat type. The female chock vocalisation type transmits less well than the male song types. Although, notice the W male song type also transmitting relatively poorly.

Differences in degradation between male song types

In the stream locations, comprising forest habitat with a more hilly terrain and the noise from the stream itself, it seems the H and L song types propagated better than the W song type. It is important to remember that the W song type is characterised by the widest band width and double whistle structure, when compared to the other two male song types.

Song vs call propagation for female vocalisations

Loud Keck calls are produced in a series by Yellow-breasted boubou females in an alarm type context, with no direct observations of this call being given by males (Wheeldon et al. 2020). Keck propagation parameters were not included in the main analysis presented in tables 3.9 – 3.11, but instead, the Keck call was compared to the female Chock song, in terms of their propagation characteristics. The Keck calls degraded more than the Chock song in all habitat types and at all distances (Fig. 3.11). The largest differences between these two different vocalisation types were for SNR, while the EA and TSR did not have any significant effect. In addition, this difference in SNR was relatively small in the shrub (~2 dB) and stream locations (~3 dB) while in the forest there was the largest average values of ~7 dB.

Stream noise

The experiments assessing the position of the receiver and sender of the signal in relation to a source of abiotic noise (a stream) found importance in these relative positions (Table 3.11, Fig. 3.12). As mentioned in Methods, the loudspeaker and microphone were only 25m apart for these experiments, with no obvious obstacles between them. I found that if the receiver was located close to a stream (i.e. a source of substantial abiotic noise), the signal arriving to the receiver had significantly lower SNR (~5 dB) in comparison to if the signal was transmitted near a stream but receiver at a further distance (Table 3.11). Therefore, the net effect of sound masking and attenuation of acoustic signals is strongly affected by the stream noise, with the precise location of the sender and receiver in relation to this being crucial. However, in contrast with the SNR, the EA and TSR did no differ significantly between the FROM STREAM and TO STREAM transmissions, which suggests a weaker effect of location on the energy loss and quality of sound revealed by tail to noise ratio. Significant distances between male and female songs were found for all song degradation measures, which suggests a stronger effect on female than male vocalisations for a receiver located closer to a stream.

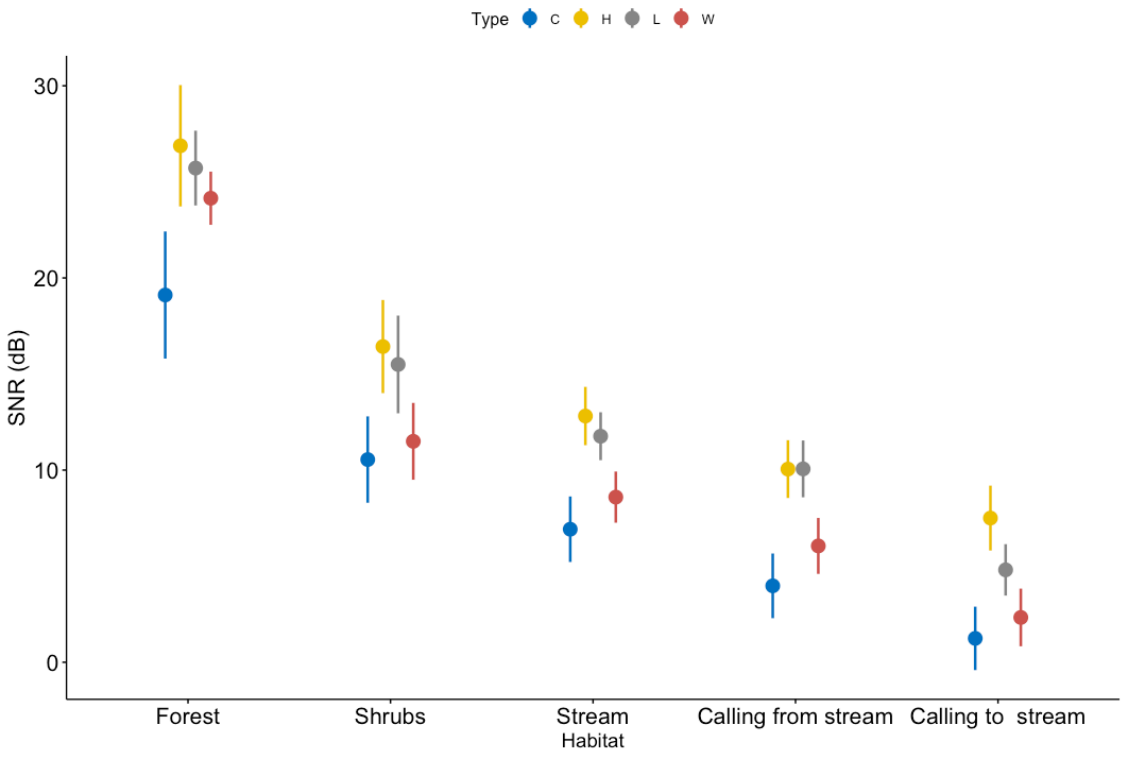

Fig. 3.12. SNR of male and female songs sang from the stream and toward the stream. These are also compared with the other 25 m propagations for the different habitat types. In all scenarios the female chock vocalisation type transmits the least well.

Table 3.11. Result of the general linear mixed model for signal-to-noise ratio (SNR), excess attenuation (EA), tail to signal ration (TSR) of propagated songs of the Yellow-breasted boubou (*Laniarius atroflavus*). Main and two-factor interaction effects are presented for the following source of variation: sex (male, female), location (transmissions FROM STREAM and TO STREAM). Both transects were done on a distance of 25 m only, close to the stream noise and with opposite location of loudspeaker and microphone in each transmission.

Source of variation	Coef.	Std. Err.	*t*	*P*
	SNR (dB)			
Main effects				
Sex	14.85	1.909	3.89	**<0.0001**
Location	-2.72	0.338	-8.05	**<0.0001**
Two-factor interaction effects				
Sex × Location	-0.65	0.356	-1.83	0.067
	EA (dB)			
Main effects				
Sex	-16.27	4.462	-3.64	**0.0003**
Location	0.90	0.862	-1.04	0.297
Two-factor interaction effects				
Sex × Location	1.62	0.91	1.78	0.075
	TSR (dB)			
Main effects				
Sex	11.85	2.835	4.18	**<0.0001**
Location	-0.49	0.584	-0.84	0.3993
Two-factor interaction effects				
Sex × Location	-3.09	0.614	-5.03	**< 0.0001**
	RTD			
Main effects				
Sex	-7.836e-04	4.768e-04	-1.64	0.1008
Location	-2.805e-04	1.016e-04	-2.761	**0.0059**
Two-factor interaction effects				
Sex × Location	2.110e-04	1.069e-04	1.974	**0.04891**

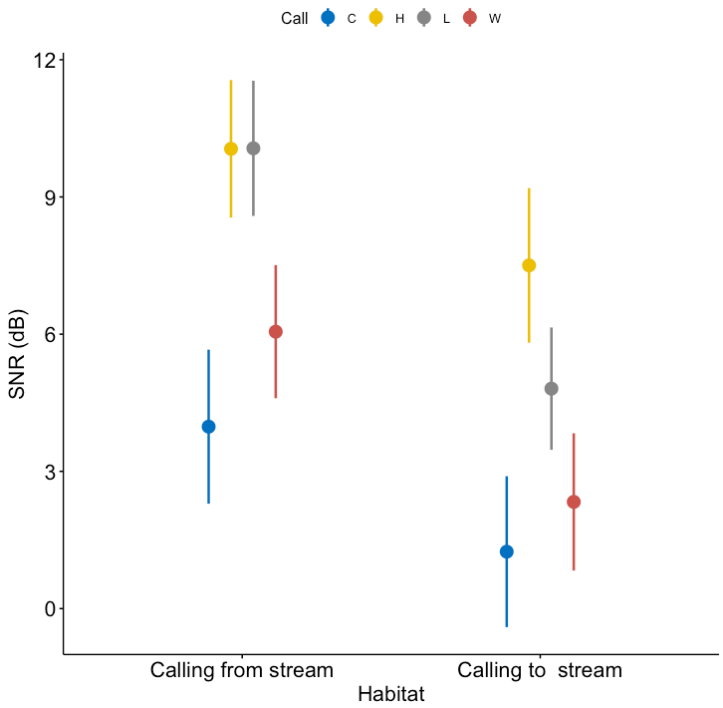

Fig 3.13. SNR of male and female songs sang from the stream and toward the stream (a zoomed in section of Fig. 3.12).

The sex differences in SNR are obvious and consistent for all habitats. Surprisingly, the differences between habitats at a relatively small distance of 25 m may reach as much as ~20 dB. Although significant differences have been observed for the different habitat types alone, it seems the shape of the terrain, vicinity to a stream and location in relation to stream noise and signaller are important to consider for song degradation (Fig. 3.13).

DISCUSSION

In the aforementioned observations and experiments the results indicate that a simple, shared, sex specific repertoire can in-fact lead to a vast array of signals utilised in within or between pair communication. Although duetting behaviour is not the prominent form of acoustic behaviour in this species, the reactions to duetting, and the variety of reactions depending on the specific duet type, suggest a multifunctional usage of this somewhat unique behaviour. In addition, the aggressive motivation of matching certain song types enhances the signals that can be transferred to conspecifics.

Calls and Songs of the Yellow-breasted boubou: Structure and Meaning

Solos

The natural repertoire of the Yellow-breasted boubou was found to be small and sex specific, with these sex specific songs being used in both a duet and solo context. The males of the study population share three whistle like phrase types which are produced in a repeated pattern that has a surprisingly fixed rate, both between phrases (later song types) and between individual males. These three song types were utilised in both solo and duet bouts. Unlike the males, females produce five specific, atonal and harsh notes when vocalising. However, they do not all function as song units in both duets and solo bouts. Three of the song types are used in solos and duets (Chock-series, Chocks, Kee-roo) whereas the Rasp call was extremely rare and was never synchronised in a duet with a male song. It is most likely that this vocalisation type is a high excitation call, evidence of this has been observed where rival pairs approached a speaker after a failed experiment and utilised this song type. The final vocalisation type in the female repertoire is the Keck type which was produced almost exclusively as a solo. Based on both visual observations of calling females close to nests and spectrograms from the array recordings, this call type seems to be produced in an alarm context.

Duets

The duets of the Yellow-breasted boubou are sex specific, with the individual male and female components being easily identifiable, even from a long distance. In a review, Hall (2004) summarises that the features of loud, locatable and sex specific duet elements support the hypothesis for the maintenance of contact between paired individuals. It would therefore seem that at the basic level, the duets of the Yellow-breasted boubou have this function, especially

useful in the visually occluded environment they inhabit. The rules behind the organisation of the study species' duets are relatively simple: 1) Both sexes can start a duet although males do so more frequently, 2) male phrases are always produced with a very regular pattern while females add one or more phrases per single male song phrase, 3) duets can be initiated with any kind of the sex specific song phrases, however, the female chock-series are never produced within a duet bout, 4) most duet bouts consist of a single type of male and female phrase, 5) if females start the duet bout they produce more phrases than males. As previously mentioned, the maintenance of pair contact is a viable function for duets in the Yellow-breasted boubou, however, although duets are produced at a large between-individual distance, they are also produced in close proximity to one another, where no partner location would be needed. The properties of sex specific, loud and locatable duets are also attributed to mate guarding as well as joint resource defence, dependent on the context (Hall 2004). Later, thorough summaries of duet functions in relation to context will be provided.

Sex specific song types

The function of duets often links with the level of sex specificity of duet repertoires, which is obviously different for different species. Although Yellow-breasted boubous possess a sex specific repertoire that is used in both solo and duet bouts, the situation within the *Laniarius* genus itself is more complicated. The Gabela bush-shrike and the Red-naped bush-shrike (*Laniarius ruficeps*) are two species in the genus where the males and females produce phrases of a similar structure, and therefore do not have a sex specific repertoire to use in duets (Fry 2020b; Fry 2020c). Similarly, the Southern-boubou (*Laniarius ferrugineus*) is a species in which males and female are able to exchange song phrase types when duetting (Wickler & Seibt 1982). Although these species show no sex specific repertoire usage, the Tropical boubou and the Crimson-breasted gonolek are two species, like the Yellow-breasted boubou, that utilise this (Grafe & Bitz 2004a; van den Heuvel et al. 2014a). In fact, like the study species, Tropical boubou males produce whistle like notes whilst females produce atonal notes when performing duets (Grafe & Bitz 2004a). In certain duetting species that do not have size or plumage dimorphism, the ability to produce sex specific song types is a way that duet members can establish mate guarding behaviours through sex recognition (Hall 2004). The mate guarding function of duets has been described in the Tropical boubou (Grafe & Bitz 2004a) and the Crimson-breasted gonolek (van den Heuvel et al. 2014a) and so it is likely that the sex specific songs of the Yellow-breasted boubou also function as mate guarding behaviour in this monomorphic species. Looking once more at the *Laniarius* genus as a whole, when comparing any existing data on vocal behaviours (Winkler et al. 2020), the majority of males seem to produce whistle like songs and females produce atonal harsh notes. With this, there may be other

functions behind the specific structure of the song types. Information on the structure of songs is provided in the methods section.

Diurnal pattern of vocal activity

As well as sex specific repertoires, the temporal pattern of song production is another aspect of duetting behaviour that is necessary to understand specific functions. Using array recordings it was possible to analyse whole day activity for various pairs as well as look at whole year activity. Yellow-breasted boubous produce the classic diurnal pattern of song production, with a clear peak in the hours around dawn as well as a peak around dusk. White-eared ground sparrows (*Melozone leucotis*) are another duetting species that show this same pattern of vocalisation production during the day (Sandoval et al. 2016). Although diel variation in vocalisations is shown, Yellow-breasted boubous do not show diel variation in duetting behaviour, in fact, the diel variation is largely due to the way in which male solos are produced. This is similar to the Tropical boubou which produces 12 different duet types, with none of them showing consistent variation throughout the day (Grafe & Bitz 2004a). When focusing on the vocalisations being produced within these peaks, it is important to remember how the dawn chorus (the main peak of vocalisations around dawn) is used by various bird species as a vast communication network. Within this network, signals can be transmitted to specific receivers but information can also be gained through eavesdropping behaviour by conspecifics (Burt & Vehrencamp 2005). Looking specifically at the large peak around dawn produced by Yellow-breasted boubous, it seems that the first vocalisations produced are usually male solo songs, followed by female solos and finally duets. An interesting find is that the least frequently produced male song type, Hwee-hwee, was usually the first vocalisation type produced. The Banded-wren is a species that uses a specific song type as the first song sung in the day. These songs are usually longer and have a higher bandwidth than other songs in their repertoire (Trillo & Vehrencamp 2005) and so it may be that certain parameters of the Yellow-breasted boubou Hwee-hwee song make it preferable for the early morning song type. However, this song type is not given exclusively at dawn and is not drastically different to the other male song types. It is possible that the dawn chorus in the study species has a duel function. The initial male solo vocalisation, and then the females eventually joining these solos to form duets, could act as type of contact song, transmitting this signal to both within-pair and between neighbours. This is similar to White-eared ground-sparrows that demonstrate pair bond maintenance through the utilisation of solos as the first vocalisation type produced in the dawn chorus (Sandoval et al. 2016). An alternative function for the use of male solo songs as the first song type could be as a way of assessing male fitness to form extra-pair copulations, as described for Black-capped chickadees (*Poecile atricapillus*) (Gammon 2004). However, Yellow-breasted boubou pairs are described as utilising a monogamous breeding

system (Harris & Franklin 2010) and so male solos as the first song type sung is unlikely for this function. It is most likely that they are used for pair-bond maintenance or territorial defence.

Although all three male solo types show diel variation in the form of a dawn and dusk chorus, there is only one female solo that shows any diel variation in its production. The Keck call is most often produced at the end of the day and with a high calling rate. This call type was often observed when human observers were close and was usually followed by the appearance of the male (personal observations) and so it is likely that it is performed in an alarm context. Langmore (1998) has previously explained that certain song types of females may be produced in order to coordinate the care of young, and so it may be that female Yellow-breasted boubous are performing these solos of diel variation to synchronise certain behaviours with their mate. It could be possible that the alarm context of this vocalisation type could in fact be to entice their partners attention.

Regarding the study species, the differences in durations of male and female unanswered solos suggests that males regularly produce long bouts of solos which often gain a response by neighbouring males or pairs. Conversely, it is likely that the short duration of female song bouts is because they are merely trying to evoke a response from their partnered male and so stop singing sooner if there is no response. It is therefore apparent that there is a dichotomy of vocal activity for males and females of the Yellow-breasted boubou. Females vocalise less than males in both solos and female initiated duets, but the amount that females sing in the tropics varies across species. Chirruping wedgebill females have a lower vocalisation production compared to males (Austin et al. 2019). It is thought that females have this low vocalisation rate, but if a mate dies they will increase their song output in order to independently defend the territory (Langmore 1998). Conversely, the Slate-coloured boubou is a species in which females have a higher singing activity than males due to their aggressive encounters (Wickler & Seibt 1979). However, it seems that females singing more intensively than males is relatively rare, with only six such species being described in the literate (Dutour & Ridley 2020), some of which are duetting species: Cocos Flycatcher (*Nesotriccus ridgwayi*; Kroodsma et al. 1987) and the New Zealand bellbird (*Anthornis melanura*; Brunton & Li 2006; Brunton et al. 2008). A reason for the difference between the amount at which males and females produce vocalisations may be due to the hormonal balance in a species, with higher testosterone levels equating to increased vocal activity (Odom et al. 2014). For Yellow-breasted boubous, the increased vocal activity of males compared to females is likely due to the reduced need for aggressive solo displays by females. In addition, the lack of intense female-female competition due to the monogamous breeding system may also be a reason as to why females are less vocal, however this needs to be treated with caution, as extra-pair offspring in a supposed monogamous breeding system has been described in a number of study species' closely related species (van den Heuvel et al. 2014b).

Pattern of response to solos and duets

Vocal and physical responses to playbacks

As well as assessing the natural vocal behaviour and gaining baseline information of the study species, we also focussed on how pairs of Yellow-breasted boubous would react to the playback of stranger(s) solos or duets, simulating territorial intrusion. When presented with the playback of a duet or a male or female solo, Yellow-breasted boubou pairs replied vocally to any intrusion type. Although both physical and vocal behaviours were performed, the usual responses were male initiated duets. The physical behaviours were the fast approach to the playback speaker as well as a close approach to the speaker. An example of the use of physical behaviours can be seen in the Rufous-and-white wren, especially the males, where physical behaviours are used in the breeding season to defend mates (Kahn et al. 2018). Vocal communication is equally important to physical behaviours, especially in dense habitats where physical displays may be visually occluded. When comparing solo and duet vocalisations, Mulder et al. (2003) suggest that Australian magpie-larks produced solos in order to deter same sex rivals and so are used as a conflict signal. Aggressive mate guarding by solo male vocalisations is also seen in Rufous and white-wrens (Kahn et al. 2018). Similarly, Tropical boubous have certain solo song types that gain a stronger response than duets, indicating that these solos are used as a mate guarding behaviour (Grafe & Bitz 2004a). Duets can also be used as a response to conspecifics, as seen in Australian magpie-larks (Mulder et al. 2003) where male initiated duets are the most common vocalisation type in response to other duetting pairs. This response is also seen in Rufous and white-wrens, with male initiated duets being used as a response to intrusions (Mennill & Vehrencamp 2008). Crimson-breasted gonoleks use their duets as cooperative signals, but when assessing the response to different sexes their duets are also used as conflict display (van den Heuvel et al. 2014a; 2014b). This perfectly demonstrates that certain species can use duetting for multiple functions and it is important to consider the context in which duets are produced as well as the intensity in order to establish conclusions of specific behaviours. With this in mind, male Yellow-breasted boubous seem to be responding to all vocalisation types as a mate guarding function, only when the female joins to form a duet are the vocalisations being used as a cooperative signal of territory defence.

By using the physical and vocal behaviours together in a response, pairs or individuals show aggression in regards to resource defence or mate guarding. The use of the combination of the two behaviour types has been described in Happy wrens when demonstrating joint territorial defence. As there is no sex bias in their responses and no heightened reaction to solitary intruders, the behaviour is deemed as a joint territory display over a mate guarding function (Templeton et al. 2011; Brumm & Goymann 2018). Yellow-breasted boubous show a large variation in

response strength for their physical and vocal behaviours. If birds demonstrated a strong vocal response this was always connected with the close approach to a speaker and duetting behaviour, which indicates the pair are displaying these signals to deter a rival(s). If focal birds had a delayed response from an increased distance from the speaker, more male solos were observed, because of this we cannot rule out pair maintenance as a possible function of duetting in the study species (Hall 2004).

Differences in reactions between solos and duets

In a range of species duets can be used as a cooperative signal (joint resource defence) or conflict signal (mate guarding). Hall (2000) assessed the difference in responses between solos and duets of Australian magpie-larks and found that they react more to duets than to solos. In this case, responding differently to solos and duets has been interpreted that males, when responding to duets, are doing so as a conflict signal. The females do not show any such aggression and so duets are likely used as a cooperative function, especially as the response to solos was the same. Other studies, on parrots (Dahlin & Wright 2012) and cuckoos (Brumm & Goymann 2018), have also concluded that if there is no difference in the response to duets and solos then duets are being used as a cooperative signal. Intruders performing duets can gain a strong response of duetting by the focal pair. Rufous-and-white wrens increase their duetting when a duet playback is introduced, highlighting the cooperative nature of duetting and the use for inter-pair communications (Mennill & Vehrencamp 2008). Multi-functionality in duets has been described in White-eared ground sparrows, if duets gain an aggressive response by a duetting pair then the functionality of this behaviour is resource defence, however, if members of a pair respond more to same-sex signallers then this indicates conflict functions such as mate guarding (Sandoval et al. 2018). Duets and male solo playback gain the strongest response by Yellow-breasted boubous when compared to female solo vocalisations, and so it is likely that duetting is a form of male mate guarding. Female solos gaining a lower response from a pair might mean that this signal is of a weaker threat and that female do not have mate guarding behaviours like the males. In fact, Yellow-breasted boubous seem to have some multi-functionality in their duetting behaviour. As previously mentioned, it seems males utilise duetting for mate guarding, however, duets getting a strong response, especially over female solos, suggests that duets are threatening and warrant pairs singing jointly in order to defend a joint resource. In addition, female answering the males to form duets may indicate a signal of commitment to conspecifics (Hall 2004).

Sex bias

It seems to fully understand the results of duetting experiments the role of sex bias is important as the reaction to different sexes can indicate whether signals are displays of conflict or

cooperation (Benedict 2010). Not only can solos or duets gain a similar or exaggerated response to the given signal, but the sex of the signaller can also gain a different response (Koloff & Mennill 2013). For some species there is a lack of sex bias towards some, if not all, vocalisation types suggesting that duetting is performed for a joint resource defence function. This was previously mentioned as a possible function for the Yellow-breasted boubou. Similarly, Barred ant-shrikes respond equally to the duet contributions of either sex, indicating that duetting functions as a cooperative signal, probably for resource refence (Koloff & Mennill 2013). Likewise, duets of Australian magpie-larks initiated by either sex gain equal responses, again highlighting the use as a cooperative rather than conflicting behaviour. On the other hand, certain species demonstrate a clear sex bias in responses, as seen in Rufous-and-white wrens, where both physical and vocal behaviours are higher towards same sex vocalisations (Mennill & Vehrencamp 2008). Yellow-breasted boubous show no such sex bias in their responses, when provided with the obvious intrusion of a stranger, indicating a cooperative function, similar to the Crimson-breasted gonolek (van den Heuvel et al. 2014a). However, even a slight bias towards a stronger female response, like the fast approach or start of the vocal response, had a strong effect on overall pair response. This suggests that females may motivate males to sing in response to intrusion.

Pair commitment

When assessing defensive behaviours, looking at experimental setup and how this might develop assumptions is important. A single speaker and two speaker setup both gained a response of defensive behaviour by the study species, however the response to the two speaker design was stronger. Approaching closer to the speaker, providing more flights and being more vocal, especially through male initiated duets, were the heightened reactions towards this setup. This difference in methodologies was also addressed for Barred ant-shrikes, where birds demonstrated a heightened response to the two speaker setup up. Koloff & Mennill (2013) suggest that the two speaker setup is deemed as more threatening, with the increased distance between signallers providing a more intense threat. As described, both experimental setups gain responses allowing various behaviours to be assessed, however, using the two speaker setup allows for more sex specific behaviours to be observed. This way of assessing behaviour is important to further understand the role of duetting in birds, especially when looking at differences in seasonal or diurnal patterns. In addition, using separate speakers means the pair commitment hypothesis can be assessed. Hall (2004) has described how, for certain species, pairs are deemed more threatening if they are separated by a larger distance whilst still being able to precisely coordinate duets. With this in mind, the two speaker playback method may represent a strong and well-rehearsed pair which in turn may be perceived as a stronger effect, resulting in the stronger

response in the results. It is also possible that the separation of the two intruders warrants a more active response from the focal pairs as each intruding individual will need to be approached and assessed. Regardless of the distance between intruding pairs, the focal pair may sing more intensively if they are out of sight from one another as a motivational function. It seems that in many duetting species, the precise timing of duets is very important (Brumm & Slater 2007). When performing complicated duets, precise coordination is a way of signalling pair bond strength (Hall & Magrath 2007) and reflects sophisticated audio-visual mechanisms of appearance (Ręk & Magrath 2020). However, the study species do not produce complicated duets, but simple duets with one pair member following the partners vocalisation with a short delay. As the timing between these phrases of duets are very stable and repeatable it seems that the coordination of duets in the Yellow-breasted boubou reflects willingness of a partner to respond rather than the demand of precise synchrony between partners (Brumm & Slater 2007). Both the single speaker and double speaker playback had the same level of male phrases overlapped by females, and so the stronger response toward the two speaker setup suggests an effect of distance in the responses given. The first explanation for this is that the separation of singing partners may be perceived as dangerous. The separation might signal communication between intruders to coordinate activities, whereas conspecifics singing close to each other may simply signal mate status, posing no threat (Grafe & Bitz 2004b). This contradicts earlier findings where close proximity demonstrates an increased threat level (Hultsch & Todt 1984) however, Yellow-breasted boubous live in a dense habitat and do not often display visually, and so the separated partners may be a more intense enemy. The second explanation is linked with the high amplitude of songs given by the Yellow-breasted boubous. On listening to birds in the field it is hard to distinguish the addition of female overlapping phrases when a male song is produced. This is especially relevant when a female chock overlaps the ascending or descending part of a male whistle. Therefore, the weaker response to closely singing pairs may reflect signal masking (Brumm & Slater 2007). It is possible that responding birds may perceive this duet as a lone male intruder, only to consider it as a pair after further signals have been detected. However, the double speaker setup may make it clearer to decipher both parts of the duet.

Meaning of male song type repertoire

Song type

Song type usage and if and how different song types are used in certain contexts is another aspect that warrants investigation when assessing duet functions. It seems that for territorial defence in the Yellow-breasted boubou the male song type, as well as the matching of male song types, is important. Strong responses to the different duet types were always linked with coordinated duetting and approaching, as explained in the previous chapter regarding response to duets and male and female solos. When presenting different types of duets to the different focal pairs there were differences in the responses provided. The WC duet playback gained the strongest response of the three duet types, reflected by number of duets produced, closest distance and time spent near speakers. When considering baseline knowledge of Yellow-breasted boubou vocalisations, the W song type was the least frequent song type used by males and rarely answered by females in order to form a duet (25.9%). This song type was also the most common song type sung as the first song in the dawn chorus (Wheeldon et al. 2020).

The HC and LC duet types gained a weaker response from focal pairs compared to the WC duet type. Although there were interesting differences between these two types, with birds responding quicker to HC playback and staying further from the speakers with LC playbacks. These results are interesting when compared to the baseline vocal information from daily and year round data (Szymański et al. 2021). The song type H is the most common song type of Yellow-breasted boubou males when breeding (42.3% of all male song bouts) and is most often produced as a solo, only being joined by females to form duets in 26.7% of all the H bouts produced (Wheeldon et al. 2020a). Therefore, we hypothesise that this H song type is primarily used to transmit a signal of territory occupancy from a distance. When considering the L male song type, this is less commonly used than the H song type, however, it is more often answered by females to form a duet (64.6% Wheeldon et al. 2020a). In addition, in the relatively rare cases when females would initiated a duet, the L song type of males was often used as the duet response. In fact, Szymański et al. (2021) revealed that during an entire year, the L song type is the male song type most often found in duets, suggesting that this song type may be important for within-pair communication. Birds responded to the LC duets with a longer latency than the HC duet type and stayed at a close distance to the speaker for a shorter amount of time. Considering this, it is more likely that the LC duet type is used for within-pair communication when compared to the HC duet type that may be used for signalling towards neighbours and intruders.

Coordination of duets requires attentiveness to the partner and so the strong response to the WC duet type may be a signal both to the partner as well as to rivals (Hall 2009). The weaker

responses to LC and HC duets suggests that there is little difference in the information being transferred, in the context of territory defence.

Song-type matching

The matching behaviour demonstrated by Yellow-breasted boubous in not random as pairs reacted stronger towards playbacks if the song type was matching. It is important to understand that the males were matching the male part of a duet, and that the male and female respond strongly together if the opposing signal was matched. This is interesting when compared to the aforementioned song type usage when naturally signing during the breeding season (Wheeldon et al. 2020) as well as the year round singing activity (Szymański et al. 2021).

The HC duet type gains a weak response and does not gain a strong response as long as the responding male does not match the song type of the intruder. However, the matching of the H song type was found to be less frequent than expected by chance. Out of 18 HC playbacks a match or between 6-10 times was expected, however, there were only 2 cases of matching. Similar to the HC duet types, if the LC duet type was matched then the response was slightly elevated, however, this matching was uncommon in only 3 cases of all playbacks produced.

Although the WC duet type gained the strongest response compared to the remaining two male duets, there is a question as to whether the response is towards the specific duet type or whether this strong response was due to males matching this song type more often? The W song type was matched more often than expected by chance (9 times), suggesting a non-random pattern. Therefore, it seems that although there is the increased response to this duet type, it is most likely due to the response of male matching behaviours. Focal birds responded to this duet type by approaching closely, suggesting their readiness for a physical attack. The fast and close approach should be considered a greater threat because such direct proximity gives real possibility of attacking the opponent (Searcy & Beecher 2009).

There was no evidence that the different male components of duets were directed to different receivers (male or female). If birds responded to playback then both pair members joined duets to jointly defend their territory. The only obvious difference between sexes was in the few experiments using the HC treatments with males producing more solos than females as a response. However, the difference was not statistically significant when considering the full model for solos ($P = 0.112$) and most responses were in fact duets. These results coincide with the results of the previous chapter whereby there is a similar strength in response towards duets and male solos with female solos gaining a weaker response. The use of the three different male duet types further supports the result that regardless of song type used, males and females defend their territory together when conspecifics are intruding upon their territory. This does not

excluded the possibility of duets being used as conflict behaviours between mated pairs, as females may vocalise less to force males to be attentive (Tobias & Seddon 2009).

Consideration of communication networks

Considering both the effects of song type and song type matching with the aforementioned song type usage (Szymański et al. 2021), an interpretation of the Yellow-breasted boubou communication network can be assessed. It is clear that the males are the sex with the leading role in vocal communication (Szymański et al. 2021) and that these are transmitted towards neighbours, strangers and mates. Whereas the females are performing vocalisations to gain responses from their partners, rather than to signal to other females or non-mated males. Female song evokes a weaker response from conspecific pairs and usually stops if their mate answers them, but this lower level of vocal behaviour does not mean that this behaviour is not important. Females have been observed to perform high excitation songs which may be to jam a partners signal in a behaviour of sexual conflict (Tobias & Seddon 2009). However, this seems unlikely in a species that protect year round territories and utilize a monogamous breeding system. Szymański et al. (2021) even indicate that the peak of female solo activity is the end of the breeding season, and so this function of female song production is unlikely.

Unlike the females, male Yellow-breasted boubous utilise their small but fully shared repertoire in a more complex system of territory defence. They are able to signal willingness for aggressive interactions, similar to other aggressive signalling systems (Wagner 1989; Waas 1991), as well as inform conspecifics of territory occupancy. In summary, the male repertoire and its use in duets, is used for territory defence, which is perceived as being more or less aggressive depending on the matching behaviour or even the specific song type used (song structure).

Interpreting the meaning of specific signals can be problematic as signals perceived as being aggressive could in fact be submissive signals (Bradbury & Vehrencamp 2011) or other aspects of behaviour (Jakubowska & Osiejuk 2018). There are a couple of frameworks that can be addressed in order to assess the problem of signal meaning. Firstly, Searcy & Beecher (2009) suggest that an aggressive signal must meet three criteria of context, prediction and response. In an aggressive context the signal should be more frequent, it should predict the escalation of the conflict by the sender and it should change the targeted receivers behaviour. When assessing responses to the different song types and song type matching all these criteria could not be tested, but it seems when examining matching behaviours and the responses, the prediction criteria was met. A differing framework was proposed by Vehrencamp et al. (2007), who suggest that a signal's meaning should be analysed by both the signaller and the receivers perspective. By testing reactions to song type and song type matching it was possible to address the receivers perspective of a signal's meaning, as different duet types gained a different response. The

meaning of the signal for the signaller was not tested but certain inferences can be made based upon correlations between signal characteristics and other behaviours of the focal birds. The fact that responding birds responded more strongly if they matched the playback suggests the perceived meaning of the signal. Especially in the case of the W song type with its heightened reaction in terms of approach behaviour. These results are similar to those of the Banded wren where vocal and physical behaviours may show different response patterns depending on the level of threat provided by the intruding signaller (de Kort et al. 2008). There is, however, an important difference between the Yellow-breasted boubou and the Banded wren in that, banded wrens deterrent value is constrained by a relationship between rate and trill bandwidth (de Kort et al. 2008). Whereas Yellow-breasted boubou males are all able to produce the different song types within their shared repertoire, with the rate of song production varying little both within and between individuals. This may indicate a different mechanism for the song type signalling between both species. Yellow-breasted boubous have song functions of a conventional character compared to the Banded wrens that are limited by production costs of signals (de Kort et al. 2008; Ręk & Osiejuk 2010).

Song matching in other duetting species

For duetting species, the function of duet repertoires is unknown, especially when considering song type occurrence and matching. In fact, matching behaviour can only occur when there is a shared repertoire between individuals. The Song sparrow is a temperate bird species that exhibits such behaviour, utilising its moderately sized repertoire in matching behaviours (Akçay et al. 2013). Similar to the Song sparrow in repertoire size is the Rufous-and-white wren, a neotropical bird species with 8-11 song types (Mennill & Vehrencamp 2005). Moser-Purdy et al. (2019) investigated whether this species match songs in an intentionally aggressive manner and so more than expected by chance. Song matching towards same sex rivals was not found for the Rufous-and-white wren even though song sharing between neighbours occurs. In addition, response strength was similar towards shared and unshared songs, and so it is unlikely that the matching behaviour demonstrated by this species is a conventional signal used in territorial conflicts (Moser-Purdy et al. 2019). This is unlike the Yellow-breasted boubou, where the small, shared repertoire of 3 male song types demonstrates matching behaviour, especially for the specific W song type. Rather than signalling aggression, matching behaviour can be used for between pair communication as seen in the Happy wren, a neotropical duetting species with a large repertoire (Templeton et al. 2013). However, the Plain wren (*Cantorchilus modestus*) is another species with a large, sex-specific repertoire that uses song matching for strengthening defence when exposed to a territorial intrusion (Mann et al. 2003; Marshall-Ball & Slater 2004). These species differ from the Yellow-breasted boubou in that they produce a larger repertoire of song types. In

addition, they seem to use the matching behaviours for between pair communications, rather than to signal aggression to same sex intruders, as is the case for the boubou.

A species with a similar sized repertoire to that of the Yellow-breasted boubou is the Eastern whipbird (*Psophodes olivaceus*). These possess sex-specific song types which are combined to form duets, exclusively initiated by males (Rogers 2005; Rogers et al. 2006). However, unlike the Yellow-breasted boubou, they perform individually specific duets (Szymański et al. 2021). There are sex differences in the matching behaviour for this species, with males matching the song type of a same sex rival and females matching the song type of their partners (Rogers et al. 2006). With this difference in matching behaviours between members of a pair, it is unlikely that matching behaviour is purely cooperative in this species. It is suggested that there is a sexual conflict and so females produce the same song type as their partner in order to deter rival females (Rogers et al. 2006).

When considering matching behaviours in the study species, it is important to look at repertoire size and sharing in similar species. Within the *Laniarius* genus, males producing whistles and the females producing harsh notes seems to be the favoured signal type (Winkler et al. 2020). However, between all of the species there are important differences in the song types produced. The Gabela bush-shrike, Red-naped bush-shrike and the Southern boubou are all species that freely share their repertoires but show no sex specific song types, an obvious difference to the Yellow-breasted boubou system. In contrast, the Slate-coloured boubou is a species which possess small sex specific repertoires, with males producing 4 song types and the females just 1. The different duet types formed by these sex specific song types have different functions such as breeding synchrony, territorial defence and mate guarding (Sonnenschein & Reyer 1983), with the links between song type and song function being much more straight forward than in the Yellow breasted boubou. In the Slate-coloured boubou, only males change their song type depending on the duet, as the female only has a single song type, and so these cause the different functions. This contrasts with the Yellow-breasted boubou system where all male songs are produced throughout the whole year and through the entire day, apart from the W song type with its strong response and favoured time of dawn chorus singing. A *Laniarius* species that differs from the aforementioned ones is the Tropical boubou. This species produced much larger repertoires with the sexes providing varying contributions to duets. Functions for the duets they produce include mate guarding and territory defence, with a specific duet type even being produced as a post conflict display (Grafe et al. 2004; Grafe & Bitz 2004b). It seems that compared to the Yellow-breasted boubou, having a larger repertoire allows for more specific duet usage to convey differing signals.

How male and female vocalisations propagate through the environment and how this affects communication

Song Propagation in different habitats

Montane forest as a habitat for song transmission

As discussed in the introduction and methods section, the Yellow-breasted boubou is a species endemic to montane forests, inhabiting elevations ranging from 700m asl to 2900m asl, the latter being the preferred altitude level (Fry 2020a). The montane forest habitats of Cameroon and Nigeria are growing at a range of altitudes at different locations and so on a macro-scale (the various mountain ranges) and a micro-scale (different relief etc.) there are various environments in which sound will transmit through. The propagation experiments conducted in the forest habitat should be considered as the ideal conditions, in terms of sound transmission, for the study species as there is flat terrain, a closed canopy of up to 25 m and a relatively open understory. This being similar to montane cloud forest habitat with *Carapa* tree species (Sainge et al. 2019). The properties of the forest habitat type mean there are relatively few obstacles such as tree trunks and dense foliage to affect signal transmission, as vegetation cover was only 20%. In addition, the forest habitat type is relatively free of spatial and atmospheric changes in comparison to open areas, these strongly affecting the degradation of signals (Wiley & Richards 1978). Within the study area itself, fragments of this forest type were relatively rare and there were issues with finding fragments large enough for the 100 m transmission distance. The more realistic habitat type in terms of availability and size was the stream location. This habitat type had diverse elevations for recording locations, stream noise and a more patchy understory.

There was a large difference in the song degradation between the forest and stream locations. Firstly, in the level terrain of the forest habitat locations, the vocalisations of both sexes propagated to 100m with a stable decrease in SNR (Fig. 3.14). However, in the stream habitat type with a more variable terrain, it was not possible to measure song degradation at 100 m from the source. The SNR for the stream locations decreased substantially more than for the forest (9 dB) even when measured at the closest distance of 12.5 m. After 25 m transmission distance the difference in the SNR for the two habitat types was vast (~14 dB). Interestingly, the pattern of degradation was uneven in terms of the distance travelled, with the SNR values for songs being less degraded after 50m (3 dB) than after 25m of transmission. This difference is probably due to the different micro-locations of the various recording points, the recording taken at 25 m in the stream habitat was in a terrain depression while at 50 m the elevation was similar to that of the loudspeaker. This situation is typical for signals transmitted in heterogenous habitats that consist of a mosaic of patches which may have different effects on the effectiveness of signal transmission (Gish & Morton 1981; Nemeth et al. 2001).

One of the factors on sound transmission that was not tested for was the perch height of the signalling and receiving individuals. Generally, this is the method in which transmission qualities are measured (Barker 2013) and is described as being a relatively simple method for such complex behaviour (Nemeth et al. 2001). The height-dependent degradation of acoustic signals in a forest are regarded as an important selection pressure for the transmission of avian vocalisations, with the variation in terrain in montane forests only amplifying the differences in transmission qualities that already occur (Nemeth et al. 2001).

It is obvious that within the forest habitat locations there are many combinations of signaller and receiver that may have affect the transmission of signals in different ways. Comparing the forest and stream sound transmission properties for an endemic montane bird species that inhabit a wide range of canopy heights, it is clear there is great potential for Yellow-breasted boubous to optimise the signal range by choosing specific locations within a habitat. Studies on other forest species such as the Eurasian blackbird (*Turdus merula*; Dabelseen et al. 1993) and the Eurasian wren (*Troglodytes troglodytes*; Holland et al. 1998) have found that perch can be utilised to aid propagation of sound signals. Therefore, in mountain areas with a range of hills and therefore a range of terrain height, this could aid the propagation of acoustic signals much like the aid provided by perch height.

Song propagation in deforested habitat

The propagation in shrub habitat was conducted in re-growing forest that had previously been burnt or felled. These habitat types have a completely different vegetation structure to that of montane forest, but unfortunately, due to human induced activities, this habitat type is dominant in areas once prime with montane forest. In general the untouched forest remnants only remain along the network of streams, the shrub areas surrounding the remaining forest patched are still suitable for breeding Yellow-breasted boubous. The propagation transects within the shrub habitat were located in a typical area of vegetation structure comprising herbs and bushes that provided nearly 100% coverage from the ground to a height of 1.5 – 3 m height. Only a few scattered trees occur within this dense vegetation cover and so it is an open canopy possessing greater micrometeorological instability than the forest habitat. Winds can add random amplitude fluctuations and scatter noise, especially during midday, both of which can affect signal propagation (Wiley & Richards 1978). The vocalisations of the Yellow-breasted boubou propagate significantly worse in the shrub than in the forest locations. Compared to each forest transect, the SNR was the lowest after 50 m (~7.1 dB) and the acoustic signals were unable to be measured at 100 m from the source. Like the forest transmission experiments, degradation in the shrub habitat was predictable between the different distances, unlike the stream habitat experiments.

The effect of stream noise on acoustic signal propagation

Abiotic noise should be considered when assessing the propagation of acoustic signals in the environment. Within African montane forests the sources of abiotic noise are wind, rain and the systems of streams. In fact, when assessing whole year recordings of the study species, strong wind and rain activity caused the birds to stop singing (Szymański et al. 2021). Certain characteristics of stream noise make this source of abiotic noise an interesting factor to assess in terms of signal evolution. Firstly, a grid system of streams are widespread in the study area, making them a spatially variable factor. Secondly, as certain streams only occur in the rainy season, remaining dry for the rest of the year, they are a variable in time, with the noise created by them reflecting the amount of previous rainfall. Although the noise created by streams may negatively influence the transmission of acoustic signals given by birds, the direct surroundings of streams are likely the best habitat for a variety of bird species due to the high productivity and food availability. This is especially true when the remnant forest patches are only located along streams (Nana et al. 2014).

Comparing the song degradation between the forest and stream habitat types does not allow for the separation of the effect of stream noise or terrain (Table 3.9). However, the experiments assessing propagation to and from the stream (STREAM TO and STREAM FROM) allow for a direct comparison of the close distance stream noise, with no obstacles and in two combinations of signaller-receiver locations. It appears that the close vicinity to stream noise has a strong deterioration effect on songs and that this is stronger for wider frequency bandwidth sounds, such as the female songs and the W male song type. In addition, the positions of signaller and receiver in relation to the source of the abiotic stream noise is also important in terms of how songs are degraded. Being a receiver located close to the source of noise resulted in ~6 dB higher SNR ratio than the converse location, for a song that was produced 25m away (Fig. 3.10). Sueur et al. (2019) describe how abiotic factors such as stream noise or wind can affect the transmission of acoustic signals in the environment. They continue to explain how climate change may be causing an increase in certain abiotic factors and this will result in an increased impact on the acoustic propagation of signals for a variety of animal taxa. An example of this can be seen with elephant vocalisations. Larom et al. 1997 found that elephant vocalisations change dramatically throughout an entire day due to the changes in abiotic factors, such as wind and air temperature. It seems certain conditions were more or less optimal for specific elephant vocalisations. When considering the Bamenda Highlands, intense human activity in the form of deforestation, causes the Yellow-breasted boubous to inhabit a narrow corridor of preferred habitat, which is left along the grid system of streams. Due to this anthropomorphic effect, the study species live in a habitat in which there is elevated ambient noise, which will ultimately affect the sending and receiving

of certain acoustic signals. A recent study assessing the effect of urban noise on bird song suggested that the birds found in urban locations have use shorter whistles, faster trills and narrower bandwidths than their rural counter parts (Phillips et al. 2020). These findings are encouraging in terms of species evolving to new acoustic environments.

Differences in propagation of male and female vocalisations

Male songs propagate further

Male songs degraded significantly less than female songs in all the conditions tested, the songs of each sex being played back at the same amplitude. The amplitude used was within the natural range of both sexes, however the range of amplitudes is moderately large and in general females do sing more quietly than males. In addition, males can exceed the amplitude used in the playbacks and therefore, the typical differences in the active signal propagation range of male and female vocalisations could be even larger than it was possible to detect in the propagation experiments.

The differences in the signal propagation for male and female Yellow-breasted boubous was expected due to prior knowledge on how different sounds degrade with transmission (Wiley & Richards 1982; Naguib & Wiley 2001; Wiley 2015) and how this can be related to the sounds produced by males and females of the study species (Wheeldon et al. 2020). The narrow frequency bandwidth characteristics of the H and L male song types allow for less degradation than the wider bandwidth of the W song type and all female vocalisations. However, the question as to why males and females vocalise so differently is not easy to answer. Usually, when comparing vocalisation types, large differences are found when comparing different species, revealing ecological adaptations to acoustically different habitats etc. (Ręk & Kwiatkowska 2016). However, only a single species is being studied here, with both sexes occupying and defending the same territory, and therefore same habitat type (Wheeldon et al. 2020; Wheeldon et al. 2021a; Wheeldon et al. 2021b). Thus, the causes for the structural differences in songs of the male and female Yellow-breasted boubous, and the consequent transmission properties, should be biological and linked with the specific functions.

The propagation experiments suggest that when singing at the same amplitude, the active acoustic range of a female song could be two times shorter than for a male song in a comparable condition. As previously mentioned, males sing more intensively, both as solos and as duet initiators, than female. In fact, when females are performing solo songs they usually stop vocalising very quickly (Wheeldon et al. 2020; Szymański et al. 2021). In addition, male songs have been found to possess individual identity information, whereas there is has not be supported for identity coding in female songs (Linhart et al. 2019; Wheeldon et al. 2020). When considering all of this, it seems male signals are aimed at potential receivers that are located at a distance, which could be

neighbouring pairs, intruders or their own mate. Female song that is produced at a lower intensity and halted quickly when not joined in a duet is most likely used for within-pair communication. As described for other tropical forest species (Mathevon et al. 2008; Aubin et al. 2014), the faster degradation of female songs, due to the atonal character and wide frequency bandwidth, may possess certain advantages when being used to cue the range of a signaller. A female responding to a mate may be able to signal her distance from him which, in a visually occluded environment like montane forest, could be very important. In addition, the synchronised duetting of a pair, that are in close proximity to one another, could signal to neighbours or potential intruders the status of the focal pair. As previously described, a highly synchronised response from focal pairs was most often the response when faced with a potential intruder, and so the intruders can assess the strength of the joint territorial defence abilities of the focal pair based on this duetting activity (Wheeldon et al. 2021a; Wheeldon et al. 2021b). A similar difference in the propagation properties of male and female vocalisations has been found for the Rufous-and-white wren, with female songs degrading more than male songs (Barker et al. 2009). The difference in the transmission of the male and female songs is thought to relate to the behaviour of the birds. Male vocalisations are used for long range transmission compared to the female songs that are most likely used for close contact communication with a mate (Graham et al. 2016).

Differences in propagation of male song types

As well as the differences in transmission properties of male and female Yellow-breasted boubous, there were also differences between the different male song types. In areas with more variable terrain (hilly stream sites), denser vegetation (shrub) and more abiotic noise (streams), the W song type degraded more than the H and L song types. This can be explained by the wider frequency bandwidth and the shorter duration of components of the W song type. As previously mentioned, there are functional differences between the different male song types. Firstly, the three different male song types are used with a consistent frequency (H>L>W) when produced as both solos and in duets (Wheeldon et al. 2020). The W song type is the most rarely produced male vocalisations type and is more often than expected by chance produced as a solo in the dawn chorus (Wheeldon et al. 2020). In addition, it is the vocalisation type that evokes the strongest response during simulated intrusion (Wheeldon et al. 2021b). When males are responding strongly to an intrusion they seem to intentionally match the type of song used when the W song is the type being used for playback. Different to the W type, the H song type seems to be used as a long distance "keep away" signal directed towards rivals, with the L song type being directed toward a female receiver (Wheeldon et al. 2021b). The H and L song types are aimed at receivers at a longer distance and to receivers that pose less threat. This related to the structure of the song types, with these signals degrading slower and so propagating further than the W song type. The

W song type is used in more aggressive, close proximity interactions where long distance transmission is not required. These findings are similar to those of the Whitethroat (Sylvia communis), whereby perch and flight calls used in territory defence and mate attraction had longer transmission, whereas the diving song, used for courtship purposes, had shorter transmission in order to reduce eavesdropping (Balsby et al. 2003). In addition, White-eared ground sparrows utilise two different call types for different functions which transmit differently to each other. The broad bandwidth call transmits less and is often used for close proximity communication between paired individuals and juveniles. A different, narrow bandwidth call transmits further, and this is used when pairs are foraging at a further distance and are visually occluded from each other (Piza & Sandoval 2016). These findings are similar to those of the Yellow-breasted boubou in that vocalisation types used for close proximity communication have a wide bandwidth, whereas communication aimed at long distance receivers have a narrow bandwidth. The functions of vocalisations utilise the transmission parameters.

Differences in propagation of female songs and alarm calls

The alarm calls produced by female Yellow-breasted boubous degraded more than female songs in all habitat types and at all distances measured. The main difference between these vocalisation types was in the SNR measure, whereas the EA and TSR were not significantly affected. This suggests that although there is a decrease in the quality of the alarm calls with distance, they are still similar in terms of detection to the different female songs. Alarm calls were often observed close to nest sites or during the approach into a territory by a human observer. Therefore, it is most likely that the intended receiver of female alarm calls is her mate, with the important information being encoded in the repetitive character of the call. This may contain information relevant to the level of threat of an intruder or the distance between the male and female of a pair. This has been described for White-eared ground-sparrows whereby they increase the rate of calling when an increased threat is present (Mendez & Sandoval 2017). This is similar to the boubous' behaviour, whereby calls are used for short distance communication, with the level of threat being conveyed through call rate. Information could be encoded in the number of repetitions of a short call and by the degradation level of a wide bandwidth frequency range. As described in the methods, calls are characterised as short and simple vocalisations used in a specific context such as for an alarm or begging. These are different to songs that are usually longer and more complex signals than calls and are used in territory defence or mate attraction (Hall 2009). The difference in the propagation qualities between female calls and songs of the Yellow-breasted boubou is similar to that of the Whitethroat. When assessing the propagation of different Whitethroat vocalisations Balsby et al. (2003) found that the calls had a shorter

transmission than the songs being used for longer range communication. The calls are directed towards a single receiver and so long distance propagation qualities are not needed.

Conclusions

The Yellow-breasted boubou is a duetting species in which males are more vocally active than females, with solos rather than duets being the dominant vocal activity type. The species possess a small, sex specific repertoire type used in both solos and duets. On a basic level, the fact that there is a dawn chorus effect on male solo production means that this could be interpreted as a form of within and between pair communication. In fact, male and female vocalisation types seem to possess specific functions. When assessing the naturally produced vocalisations of the study species, male solos and male initiated duets seem to be used for territory defence, whereas the female singing pattern of solos and duets suggests the targeted receiver is their own mate.

Experimental playback procedures allowed for the further investigation of Yellow-breasted boubou vocal activities and their specific functions. It seems territory owners perceive female solos as a low threat signal, whereas male solos and duets evoke a stronger response, indicating a higher threat. Strong physical responses, indicated by the close approach by focal pairs to the playback speaker, were connected with higher vocal output of male led duets. However, this joint defence was stronger if females initiated the duets or produced an enhanced vocal rate. If males were producing solos, the close physical approach behaviour was not observed, indicating that they may postpone the stronger response for when a female is present and contributes to a duet bout. The fact that male solos have the highest response of all vocalisation types suggests they are used as a conflict signal in mate guarding behaviours, whereas the high response to duetting is probably due to their function of joint territorial defence. Therefore, it highlights that Yellow-breasted boubous are able to produce multifunctional signals, depending on the intended receiver.

The comparison of one and two speaker playback methods allowed me to compare the response of focal pairs towards spatially separated or close proximity intruders. Spatially separated intruders represented a higher threat level, with focal pairs increasing vocal output and physical flight displays.

Further experimental investigation into specific song type functions indicates that males and females provide a stronger vocal response to any duet type if they matched the vocalisation type provided by the playback. The W song type, the least common male song type used, was matched most often when compared to the two remaining male song types. There was also no significant difference in response strength of either sex to any kind of simulated intrusion. These results indicate that Yellow-breasted boubous may use their various vocalisations in a hybrid way, linking coding information with phrase structure and song matching.

Following investigation into specific song and call type functions, propagation experiments were able to shed light on further adaptations of song type parameters. There were clear differences in the propagation qualities of the various vocalisation types as well as the way these are transmitted through the various habitat types in which the boubous are found. Male songs are able to

propagate further than female song and calls types in each habitat tested. This again links to the previously described functions of specific vocalisation types, with male songs being intended for distant receiver whereas female are most likely performing solos towards their own mate. The presence of abiotic noise (a stream system) effects the way in which a signal will be received, with terrain and abiotic noise having a strong negative effect on the active signal space. That deforestation is occurring in the range of the Yellow-breasted boubou, their communication system may be affected. Their natural forest habitat, where their vocalisations are best transmitted, is being reduced, with only remnant patches, mostly along streams, remaining. Instead, shrub habitat remains wherein their signals transmit less well. The stream noise and the propagation quality in the shrub habitat means that the communication system will definitely be effected, and signallers will have to adapt in order to limit degradation within these different habitat types.

Supplement

Table S1. Basic characteristics of the song and call bouts of the Yellow-breasted Boubou recorded.

Each row from 1 to 46 indicate different classes of recorded bouts. Rows in the column 'Bout type' letters indicate all combinations of vocalisations produced by the study species. E.g. 'H' in row 1 indicates that High whee-oo solos produced by males (without response from a female) were recorded 1697 times, which gives 28,6% of all bouts etc. The next row 2 indicates that we recorded 354 'HK' cases in which High whee-oo male song phrase was answered by Kee-roo phrase of a female, and this gives 6% all bouts, or 8.8% among bouts initiated by males etc.

Shades left for easier recognition between male (darker) and female (lighter) initiated vocalisations.

Contents of percentage columns: (a) % all bouts; (b) % within a sex/call type; (c) % within sex/call answered; (d) % within solos; (e) % within solos; (f) % within male or female solos; (g) % within duets; (h) % within male or female initiated duets.

No	Bout type	N	Sex of Initiator	Song or call type of Initiator	Answered	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
1	H	1697	M	H	no	28,6%	42,3%	73,3%		37,9%	60,0%		
2	HK	354	M	H	yes	6,0%	8,8%	15,3%	57,3%			24,2%	29,9%
3	HC	257	M	H	yes	4,3%	6,4%	11,1%	41,6%			17,6%	21,7%
4	HR	3	M	H	yes	0,1%	0,1%	0,1%	0,5%			0,2%	0,3%
5	HCs	2	M	H	yes	0,0%	0,0%	0,1%	0,3%			0,1%	0,2%
6	HQ	1	M	H	yes	0,0%	0,0%	0,0%	0,2%			0,1%	0,1%
7	HLC	1	M	H	yes	0,0%	0,0%	0,0%	0,2%			0,1%	0,1%
8	L	709	M	L	no	11,9%	17,7%	60,8%		15,9%	25,1%		
9	LK	326	M	L	yes	5,5%	8,1%	27,9%	71,2%			22,3%	27,5%
10	LC	126	M	L	yes	2,1%	3,1%	10,8%	27,5%			8,6%	10,6%
11	LR	5	M	L	yes	0,1%	0,1%	0,4%	1,1%			0,3%	0,4%
12	LHK	1	M	L	yes	0,0%	0,0%	0,1%	0,2%			0,1%	0,1%
13	W	421	M	W	no	7,1%	10,5%	79,4%		9,4%	14,9%		
14	WK	61	M	W	yes	1,0%	1,5%	11,5%	56,0%			4,2%	5,1%
15	WC	45	M	W	yes	0,8%	1,1%	8,5%	41,3%			3,1%	3,8%
16	WQ	1	M	W	yes	0,0%	0,0%	0,2%	0,9%			0,1%	0,1%
17	WLK	1	M	W	yes	0,0%	0,0%	0,2%	0,9%			0,1%	0,1%
18	WHC	1	M	W	yes	0,0%	0,0%	0,2%	0,9%			0,1%	0,1%
19	Cs	534	F	Cs	no	9,0%	27,8%	81,9%		11,9%	32,5%		
20	CsHK	76	F	Cs	yes	1,3%	4,0%	11,7%	64,4%			5,2%	27,4%
21	CsLK	23	F	Cs	yes	0,4%	1,2%	3,5%	19,5%			1,6%	8,3%
22	CsH	12	F	Cs	yes	0,2%	0,6%	1,8%	10,2%			0,8%	4,3%
23	CsWK	3	F	Cs	yes	0,1%	0,2%	0,5%	2,5%			0,2%	1,1%
24	CsWLK	2	F	Cs	yes	0,0%	0,1%	0,3%	1,7%			0,1%	0,7%
25	CsL	1	F	Cs	yes	0,0%	0,1%	0,2%	0,8%			0,1%	0,4%
26	CsHLK	1	F	Cs	yes	0,0%	0,1%	0,2%	0,8%			0,1%	0,4%
27	K	57	F	K	no	1,0%	3,0%	37,0%		1,3%	3,5%		

28	KL	54	F	K	yes	0,9%	2,8%	35,1%	55,7%			3,7%	19,5%
29	KW	22	F	K	yes	0,4%	1,1%	14,3%	22,7%			1,5%	7,9%
30	KH	17	F	K	yes	0,3%	0,9%	11,0%	17,5%			1,2%	6,1%
31	KHL	1	F	K	yes	0,0%	0,1%	0,6%	1,0%			0,1%	0,4%
32	KHW	1	F	K	yes	0,0%	0,1%	0,6%	1,0%			0,1%	0,4%
33	KLW	1	F	K	yes	0,0%	0,1%	0,6%	1,0%			0,1%	0,4%
34	KWHL	1	F	K	yes	0,0%	0,1%	0,6%	1,0%			0,1%	0,4%
35	C	63	F	C	no	1,1%	3,3%	53,8%		1,4%	3,8%		
36	CL	22	F	C	yes	0,4%	1,1%	18,8%	34,4%			1,5%	7,9%
37	CH	21	F	C	yes	0,4%	1,1%	17,9%	32,8%			1,4%	7,6%
38	CW	10	F	C	yes	0,2%	0,5%	8,5%	15,6%			0,7%	3,6%
39	CHWL	1	F	C	yes	0,0%	0,1%	0,9%	1,6%			0,1%	0,4%
40	Q	972	F	Q	no	16,4%	50,6%	99,8%		21,7%	59,1%		
41	QL	1	F	Q	yes	0,0%	0,1%	0,1%	0,1%			0,1%	0,4%
42	QW	1	F	Q	yes	0,0%	0,1%	0,1%	0,1%			0,1%	0,4%
43	R	19	F	R	no	0,3%	1,0%	76,0%		0,4%	1,2%		
44	RL	4	F	R	yes	0,1%	0,2%	16,0%	66,7%			0,3%	1,4%
45	RW	1	F	R	yes	0,0%	0,1%	4,0%	16,7%			0,1%	0,4%
46	RWL	1	F	R	yes	0,0%	0,1%	4,0%	16,7%			0,1%	0,4%

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